Vol. 74 JANUARY-FEBRUARY, 1947

Bulletin

of the

Torrey Botanical Club

and

Torreya

CONTENTS

Pythium Crown Rot of Rhubarb ..... John
The Production of Antifungal Agents by Actinomycetes ..... Albert Schatz
The Role of Certain Environmental Factors in Growth and Production of Pectolytic Enzymes by Klebsiella Oxytoca ..... Sister M. Laurentia
Studies in the Chrysophyllaceae—I. A Synopsis of American Species of Australia, Syst. Enumeration
Leaf Variation in Delphinium virescens
Tropidendron, Tetrocentron, and Their Meaning in
Noteworthy Plants of South America—III. Specimens
Noteworthy Plants of South America—IV. Three Ve
Paul Standley and
Noteworthy Plants of South America—V. The Ge
Torreya:
An Apparently New Species of Ginkgo
Proceedings of the Club
Index to American Botanical Literature

Published by the Club bi-monthly

[illegible] COMPANY
[illegible] AVE.
[illegible] VIRGINIA

THE TORREY BOTANICAL CLUB

Officers for 1946

President: P. W. Zimmerman

Vice-presidents: John A. Small, Henry K. Svenson

Recording Secretary: Lillebo Ajello

Corresponding Secretary: Jennie L. S. Simpson

Treasurer: Edmund H. Fulling

Editor: Harold W. Rickett

Business Manager: Ann M. Hanson

Bibliographer: Mrs. Isabella Schwarzen

The Bulletin of the Torrey Botanical Club

and Torreya

Editor

Harold W. Rickett

Associate Editors

Irving W. Bailey
Stanley A. Cain
M. A. Chrysler
Adriance S. Foster
Henry Allan Gleason
John W. Shive

for Torreya

Harold H. Clum
Lillebo Ajello

Subscriptions, dues and inquiries about back numbers should be sent to the office of publication, N. Queen St. and McGovern Ave., Lancaster, Pa., or to Dr. Edmund H. Fulling, The New York Botanical Garden, New York 58, N. Y. Correspondence about advertisements and circulation should be addressed to Dr. Ann M. Hanson, Box 12, Schermerhorn Hall, Columbia University, New York 27, N. Y. Communications about exchanges should be sent to Dr. Jennie L. S. Simpson, Hunter College, New York 21, N. Y. Manuscripts intended for the Bulletin should be sent to Dr. H. W. Rickett, The New York Botanical Garden, New York 58, N. Y. Short notes for Torreya may be addressed to Dr. H. H. Clum, Hunter College, New York 21, N. Y.

Claims for missing numbers must be made within 60 days from the date of issue.

The subscription price of the Bulletin of the Torrey Botanical Club (including Torreya) is $7.00 a year except to active members of the Club. Of the annual membership dues, $3.50 covers a year's subscription to the Bulletin.

Entered as second-class matter October 6, 1942 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in paragraph 4, section 412, P. L. & R.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 1, PP. 1–8 JANUARY, 1947

PYTHIUM CROWN ROT OF RHUBARB[1]

JOHN T. MIDDLETON

INTRODUCTION

Rhubarb, *Rheum Rhaponticum* L., is a popular early spring vegetable grown throughout most of the United States, although more commonly in the northern than in the southern latitudes. The two principal districts in which rhubarb is produced commercially are New Jersey and California.

In California most of the commercial rhubarb is grown in the San Francisco Bay area, chiefly in Alameda County, and in the immediate vicinity of Los Angeles. Rhubarb is usually planted in relatively small acreages, varying in size from one to forty acres. In northern California it is generally grown on heavy silt-loam soils, without irrigation; in southern California it is most frequently planted on relatively light, sandy, irrigated soil. Rhubarb may be harvested throughout the year in California, but the bulk of the crop is taken in the early spring, both for local use and for eastern shipment.

Crown rot of rhubarb was observed in March, 1936, in the San Francisco Bay area,[2] and in February, 1940, in the vicinity of Los Angeles. A number of plants in several fields in each of the two localities were affected, demonstrating that the disease occurs regardless of soil type and irrigation practice. Isolations from affected material yielded pure cultures of several species of *Pythium*.

REVIEW OF THE LITERATURE

A number of rots are reported as affecting the root, crown, and stem of the rhubarb plant with symptoms similar to those associated with the presence of *Pythium* spp. but due to other organisms. The one most likely to be confused with the rot caused by *Pythium* is that due to species of *Phytophthora*.

Beach (1921) described a wilt of rhubarb in which the leaves wilted, turned yellow, and collapsed, and the crown and roots became discolored and rotten; an unidentified species of *Phytophthora* was isolated from the diseased material. Beach (1922) later gave a more detailed description of the disease and identified the fungus as *P. cactorum* (L. & C.) Schroet.; several additional reports on the disease were also made (1924, 1925, 1926). Godfrey

[1] Paper No. 544, University of California Citrus Experiment Station, Riverside, California.

[2] Observation by C. M. Tompkins.

(1923) described a disease similar to that given by Beach, but attributed it to *P. parasitica* Dast. var. *rhei* Godfrey, a new variety which Tucker (1931) would abandon, since the fungus conforms with the limits of the species in the broader sense. Infection of rhubarb with *P. parasitica* has been reported in the United States by Tucker (1933a, 1933b, 1935) and by Ramsey and Wiant (1944); in the Union of South Africa by Doidge (1924) and Wager (1931, 1935, 1940); in Rhodesia by Hopkins (1931); it has also been reported in New South Wales (1943). Tucker (1933a) indicates that one of the unidentified species of *Phytophthora* from rhubarb in Illinois, described by Beach, fits the description of *P. parasitica*, though no material is available for study. Barrett (Merrill 1927) reported a decay of roots, crown, and basal portion of the petioles of rhubarb, from which a fungus resembling *Pythiacystis* (syn. *Phytophthora*) was secured.

A *Pythium* sp. was first reported from rhubarb in the United States by Drechsler (1930), who described the fungus as *P. anandrum* Drechs. and stated that it was isolated "from softened underground bud of *Rheum rhaponticum* L. collected near Brentwood, Md. . . ." Drechsler did not describe the symptoms of the disease, nor did he describe the pathogenicity of the fungus to rhubarb.

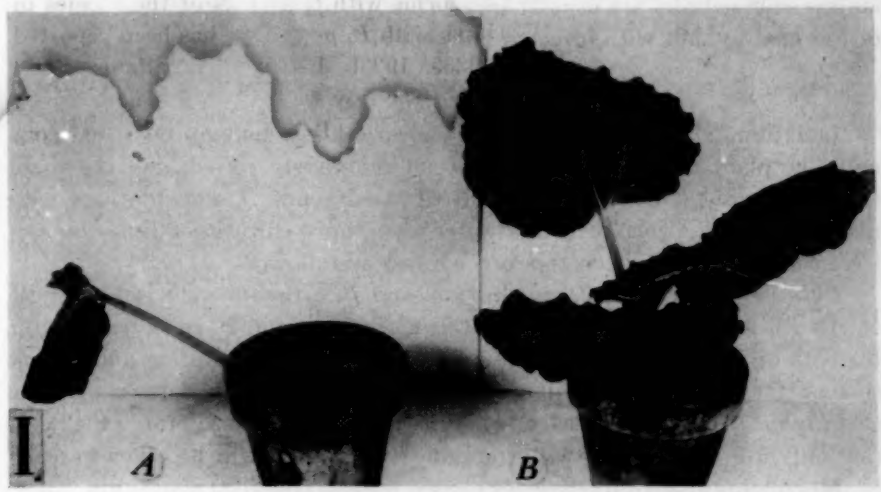
Wager (1931) reported the isolation of *Pythium ultimum* Trow, together with *Phytophthora parasitica*, from rotted rhubarb in the Union of South Africa. He established the pathogenicity of *Pythium ultimum* to rhubarb by artificially inoculating injured rhubarb seedlings grown in sterile soil. The fungus was unable to infect uninjured plants. Infected plants very often recovered. Symptoms of the disease caused by *P. ultimum* were similar to those produced by *Phytophthora parasitica*. Wager (1932, 1940) later published further reports on the occurrence of these two fungi on rhubarb.

Middleton (1941, 1943) recorded the occurrence of *Pythium anandrum*, *P. oligandrum* Drechs., and *P. ultimum* from rhubarb grown in California. Ramsey and Wiant (1944) report that *P. ultimum* and other species of *Pythium* are able to infect rhubarb.

SYMPTOMS OF THE DISEASE

Rhubarb plants infected with *Pythium* crown rot usually wilt; the leaves then turn yellow, and later collapse (fig. 1). The basal portions of the petioles of infected leaves generally show sunken, longitudinally oriented, brown streaks ¼–½ inch wide, which progress upwards about 2–3 inches. Infected crowns (fig. 2) are soft and watersoaked, with the tissues somewhat flaccid, and brown in color; the infection ordinarily progresses to the bud scales, and later to the buds, causing a blight of the shoots. Sometimes young buds escape infection despite the diseased crown, only to become infected when just at or above the soil level. Rarely does the disease develop far above

ground level, its development then depending upon a moist atmosphere. Only the roots of some plants are affected, the cortex becoming flaccid and



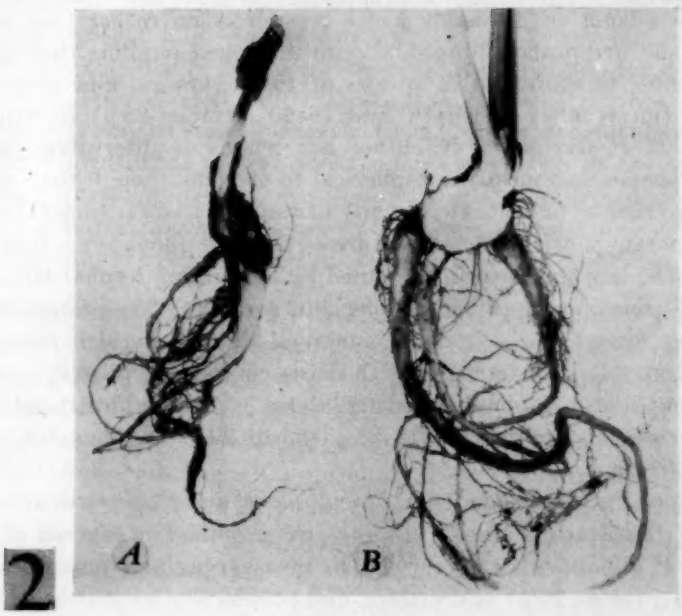


FIG. 1. A. Rhubarb plant artificially infected with *Pythium* crown rot. B. Healthy plant. FIG. 2. Longitudinal sections (A) through crown of rhubarb plant artificially infected with *Pythium* crown rot, and (B) through crown of healthy plant.

watersoaked; such plants are usually small, with spindly, somewhat chlorotic leaves and few marketable petioles. Plants with infected roots occasionally recover, but often die.

Apparently healthy petioles collected from diseased plants frequently decay after packing, the rot consuming the major portion of the remaining stalks; such petioles are usually taken from plants with shoots that are more or less healthy, but with infected bud scales.

THE CAUSAL ORGANISMS

Isolation. Isolation of the fungi concerned was made in the usual manner. The plant material selected was not completely rotted, and the tissue removed included both healthy and diseased zones. Tissue platings were normally made on corn meal and water agar; pure cultures of *Pythium* spp. were easily obtained when this procedure was followed.

Pythium anandrum, *P. oligandrum*, and *P. ultimum* were isolated first. Further isolations yielded, also, *P. irregulare* Buis. and *P. splendens* Braun, for both of which rhubarb is a new host. A detailed description and discussion of the above-mentioned species, together with their host range and geographic distribution, has already been given by Middleton (1943), so that only a brief presentation of specific information will be given here.

Morphology. All five species named possess spherical sporangia. Those of *Pythium anandrum* are typically borne terminally on rather long sporangiophores, and are prolate-ellipsoidal with an apical papilla; they thus bear some likeness to sporangia of species of *Phytophthora*, and measure about 32–85 μ (mean 50 μ) in length, and 18–40 μ (mean 25 μ) in width. The sporangia of *P. irregulare* are either acrogenous or intercalary, and are of various shapes, but mostly subspherical to obovate, though they may be ellipsoidal, pyriform, or truncate, usually measuring 10–27 μ (mean 18 μ) in diameter. Sporangia of *P. oligandrum* are of the contiguous type, formed of several more or less spherical units joined by connecting hyphal strands or merely sessile, one upon the other, the elements averaging 35 μ in diameter. Relatively large acrogenous sporangia, spherical to subspherical, measuring 21–49μ (mean 36 μ) in diameter, with dense contents, typify *P. splendens*. Acrogenous sporangia, borne on short lateral hyphae, typically spherical to subspherical, and measuring 12–28 μ (mean 20 μ) in diameter, are found in *P. ultimum*.

The oögonia of *Pythium anandrum*, *P. irregulare*, and *P. oligandrum* are spiny; those of *P. splendens* and *P. ultimum* are smooth. The oögonia of *P. anandrum* and *P. oligandrum* are very similar in size, ranging from approximately 15 to 35 μ (mean 27 μ) in diameter, and possess similar spines, which are conical in form and acutely tipped. Oögonia of *P. irregulare* may have numerous to few spines, and infrequntly lack spines, but in such instances the oögonial wall is undulate to somewhat blunt-serrate. Spines of *P. irregulare* vary in shape but are usually of broad base and acuminate apex, straight or contorted. *P. splendens* rarely produces oögonia; when present,

the oögonia are spherical and acrogenous; they vary in size from about 25 to 35 μ (mean 32 μ) in diameter, and possess a smooth, thin oögonial wall. Oögonia of *P. ultimum* are like those of *P. splendens,* but smaller in size, ranging from 19 to 23 μ (mean 20 μ) in diameter.

Antheridia are lacking in *Pythium anandrum* and are rarely present in *P. oligandrum*, then usually diclinous rather than monoclinous in origin, clavate and slightly crooknecked, with two or three transverse constrictions. Antheridia of *P. irregulare* are typically monoclinous, and vary in number from 1–4 per oögonium. When the sexual apparatus of *P. splendens* is available for study, usually 1–8 clavate and more or less crooknecked antheridia of mono- or diclinous origin are found. Antheridia of *P. ultimum* are typically monoclinous, short, and sharply upcurved, originating immediately below the oögonium and making apical contact with the basal portion of the oögonial wall; the antheridial cell is not necessarily delimited by a septum.

The oöspores of *Pythium anandrum, P. irregulare, P. oligandrum, P. splendens,* and *P. ultimum* are aplerotic, with certain differences in diameters and in thickness of oöspore walls.

Pythium anandrum may be separated from its congeners by its sporangia and spiny oögonia. *P. oligandrum* is identifiable by its contiguous sporangia and spiny oögonia. *P. irregulare* is readily recognized by the peculiar echinulation of the oögonial wall. *P. splendens* is one of the few species of the genus that may be identified on the basis of its sporangial characters, though positive identification should rest upon observation of the sexual stage or certain physiologic traits. *P. ultimum* is generally determined on the basis of its spherical sporangia, thick-walled oöspore, and the more or less unique relationship existing between the oögonium and antheridium.

Temperature—Growth Relations. The cardinal temperatures for growth of the several species of *Pythium* isolated from rhubarb were determined to be as follows (in degrees centigrade): *P. anandrum:* minimum 1°, optimum 28°, maximum 34°; *P. irregulare:* minmum 4°, optimum 28°, maximum 37°; *P. oligandrum:* minimum 7°, optimum 31°, maximum 40°; *P. splendens:* minimum 4°, optimum 28–31°, maximum 37°; *P. ultimum:* minimum 1°, optimum 28°, maximum 37°. These values conform with those given by Middleton (1943) for isolates of the species obtained from other hosts in various localities.

PATHOGENICITY

The pathogenicity of the several *Pythium* spp. to rhubarb seedlings and mature plants was determined. Plants were grown from seed sown in flats containing sterile soil; seedlings were later transplanted to 6-inch pots of sterile soil. In each test pure cultures of the fungus, grown on a mixture of sterilized whole oats and wheat, were added to the soil of three lots of 25

plants with uninjured roots, and to three lots of 25 plants with injured roots; sterile oats and wheat, only, were added to the soil of three lots of 25 plants with uninjured roots, and to three lots of 25 plants with injured roots, to serve as controls. The three lots of plants were, in each case, made up of plants of three age groups, namely, 2, 6, and 12 months, respectively. The results of the inoculation are given in table 1.

All the species of *Pythium* tested were pathogenic to rhubarb. Uninjured 2-month-old plants were more susceptible to infection than uninjured 6- and 12-month-old plants. Plants with injured roots were more readily infected than those with uninjured roots. *P. anandrum* and *P. ultimum* were equally virulent on injured 2-, 6-, and 12-month-old plants, whereas *P. oligandrum* and *P. splendens*, though equally virulent on injured 2-month-old plants,

TABLE 1. *Results of artificial inoculation, with Pythium spp., of rhubarb plants of three age groups, with and without root injury.*

Organism	Number of plants infected (of 25 inoculated)					
	2 months old		6 months old		12 months old	
	Uninjured	Injured	Uninjured	Injured	Uninjured	Injured
P. anandrum	8	25	3	25	4	25
P. irregulare	2	20	1	16	2	13
P. oligandrum	7	25	2	19	0	10
P. splendens	11	25	10	23	6	21
P. ultimum	25	25	16	25	11	25
None (control)	0	0	0	0	0	0

were somewhat less virulent on injured 6- and 12-month-old plants. *P. irregulare* was less pathogenic than the other species on uninjured and injured 2- and 6-month-old plants, and although less pathogenic than *P. anandrum*, *P. splendens*, and *P. ultimum* on uninjured and injured 12-month-old plants, it was somewhat more pathogenic than *P. oligandrum* on these plants.

Symptoms expressed by artificially infected plants are similar to those of naturally infected plants.

Isolations made from diseased tissue from artificially infected rhubarb yielded pure cultures of the organisms that had been added to the soil of the respective pots.

A few of the plants in the 6- an 12-month age groups lost a fair proportion of their leaves, yet did not die. Several of these plants began to recover some two months after their inoculation and appeared normal about three months later. Wager (1931) reported recovery of some rhubarb plants artificially inoculated with *Pythium ultimum*.

The ability of *Pythium anandrum*, *P. irregulare*, *P. oligandrum*, *P. splendens*, and *P. ultimum* to cause damping-off of rhubarb was investigated. For each of the five species of *Pythium*, 50 rhubarb seeds were sown in each of ten pots of sterile soil infested with the fungus; 50 seeds were also sown

in each of ten pots of noninfested sterile soil to serve as controls. The results are presented in table 2. All the fungi proved to be capable of causing damping-off. It is of interest to note that whereas both *P. anandrum* and *P. ultimum* were equally virulent on 2-, 6-, and 12-month-old injured rhubarb plants, *P. anandrum* is less able to cause damping-off of seedlings than *P. ultimum*, which is extremely effective. *P. irregulare*, *P. oligandrum*, and *P. splendens* cause greater damping-off of rhubarb than *P. anandrum*, but considerably less than *P. ultimum*.

TABLE 2. *Damping-off of rhubarb by Pythium spp. isolated from rhubarb.*

Organism:		*P. anandrum*	*P. irregulare*	*P. oligandrum*	*P. splendens*	*P. ultimum*	None (control)
Number of survivals (from 50 seeds sown per pot)	Pot 1	19	14	10	16	3	36
	Pot 2	25	7	2	10	1	39
	Pot 3	25	10	3	17	0	31
	Pot 4	31	9	5	21	3	35
	Pot 5	28	12	8	19	1	33
	Pot 6	26	11	10	12	3	30
	Pot 7	20	8	12	15	0	38
	Pot 8	30	14	7	16	3	36
	Pot 9	27	10	5	17	0	38
	Pot 10	23	8	9	15	0	32
Mean number of survivals per pot		25.4	10.3	7.1	15.8	1.4	34.8
Per cent stand		73.0	29.6	20.4	45.4	4.0	100.0

SUMMARY

A disease affecting the root, crown, and stem of rhubarb has been observed in the two principal rhubarb-producing areas of California. The first symptom of crown rot is a slight wilting of the plant, followed shortly by a yellowing of the leaves, with their subsequent collapse. Infected crowns are flaccid, watersoaked, and brown in color. Petioles and bud scales may also be affected; plants then appear blighted in the field.

Isolations made from diseased material yielded pure cultures of *Pythium anandrum*, *P. irregulare*, *P. oligandrum*, *P. splendens*, and *P. ultimum*. The pathogenicity of the isolated organisms to 2-, 6-, and 12-month-old rhubarb plants was established, *P. ultimum* being the most virulent of the five species tested.

Pythium anandrum, *P. irregulare*, *P. oligandrum*, *P. splendens*, and *P. ultimum* are all able to cause damping-off of rhubarb. *P. ultimum* causes the greatest reduction in stand.

UNIVERSITY OF CALIFORNIA, CITRUS EXPERIMENT STATION
RIVERSIDE, CALIFORNIA

Literature Cited

Beach, W. S. 1921. A *Phytophthora* crown rot of rhubarb. Phytopathology **11**: 55–56. [Abstract.]

————. 1922. The crown rot of rhubarb caused by *Phytophthora cactorum*. Pa. Exp. Sta. Bull. **174**: 1–28.

————. 1924. A rhubarb disease. *In:* 37th annual report of the director. Pa. Exp. Sta. Bull. **188**: 16.

————. 1925. Crown rot of rhubarb. *In:* 38th annual report of the director. Pa. Exp. Sta. Bull. **196**: 16.

————. 1926. Crown rot of rhubarb. *In:* 39th annual report of the director. Pa. Exp. Sta. Bull. **204**: 16.

Doidge, E. M. 1924. A preliminary check list of plant diseases occurring in South Africa. Bot. Surv. So. Afr. Mem. **6**: 1–56.

Drechsler, C. 1930. Some new species of *Pythium*. Jour. Wash. Acad. **20**: 398–418.

Godfrey, G. H. 1923. A *Phytophthora* footrot of rhubarb. Jour. Agr. Res. **23**: 1–26.

Hopkins, J. C. F. 1931. Plant pathology in southern Rhodesia during the year 1930. Rhodesia Agr. Jour. **28**: 384–389.

Merrill, E. D. 1927. Report of the director of the Agricultural Experiment Station. Calif. Exp. Sta. Rept. **1926–27**: 1–110. [See specifically p. 62].

Middleton, John T. 1941. Crown rot of rhubarb caused by *Pythium* spp. Phytopathology **31**: 863. [Abstract.]

————. 1943. The taxonomy, host range and geographic distribution of the genus *Pythium*. Mem. Torrey Club **20**: 1–171.

New South Wales Biological Branch, Division of Science Services. 1943. Rhubarb wilt or crown rot. Agr. Gaz. N. S. Wales **54**: 224.

Ramsey, Glen B. & Wiant, James S. 1944. Market diseases of fruits and vegetables: beets, endive, escarole, globe artichokes, lettuce, rhubarb, spinach, Swiss chard, and sweetpotatoes. U. S. Dept. Agr. Misc. Pub. **541**: 1–40.

Tucker, C. M. 1931. Taxonomy of the genus *Phytophthora* de Bary. Mo. Exp. Sta. Res. Bull. **153**: 1–208.

————. 1933a. The distribution of the genus *Phytophthora*. Mo. Exp. Sta. Res. Bull. **184**: 1–80.

————. 1933b. Identification of plant diseases. *In:* Work of the Agricultural Experiment Station. Mo. Exp. Sta. Bull. **328**: 25–26.

————. 1935. Morphologic and physiologic studies on the genus *Phytophthora*. *In:* Work of the Agricultural Experiment Station. Mo. Exp. Sta. Bull. **358**: 38.

Wager, V. A. 1931. Diseases of plants in South Africa due to members of the Pythiaceae. Dept. Agr. So. Afr. Sci. Bull. **105**: 1–43.

————. 1932. Foot-rot disease of papaws. Farming in South Africa **6**: 435–437.

————. 1935. Brown rot of tomato fruits due to *Phytophthora parasitica* Dast. So. Afr. Jour. Sci. **32**: 235–237.

————. 1940. Descriptions of the South African Pythiaceae with records of their occurrence. Bothalia **4**: 3–35.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, No. 1, pp. 9–19 JANUARY, 1947

THE PRODUCTION OF ANTIPHAGE AGENTS BY ACTINOMYCETES[1]

ALBERT SCHATZ AND DORIS JONES

The ability of microorganisms to inhibit bacteriophages is well known. With certain staphylococci, this antiphage effect may be due to the adsorption and destruction of the phage by cells of resistant strains derived from an originally susceptible culture (Rakieten 1932). The irreversible adsorption of staphylococcus bacteriophage has also been demonstrated with resistant strains of the *Bacillus subtilis* group (Rakieten, Rakieten & Doff 1936a). The capacity of bacteria other than staphylococci to adsorb or destroy staphylococcus phages has been proposed to explain, at least in part, why these phages are not commonly encountered in stool filtrates or sewage (Rakieten 1942). The phage-adsorbing capacity of yeasts and fungi has likewise been reported (Rakieten, Rakieten & Doff 1936).

In many investigations, substances which have been isolated from bacterial cells have been shown to possess phage-adsorbing or inactivating properties. Phospholipids obtained from susceptible and resistant strains of *Escherichia coli* as well as lipids of non-bacterial origin have been found inhibitive to bacteriophagia (Williams, Sandholzer & Berry 1940). A general rather than a selective inhibition has also been reported for various cholera phages with lipids from cholera strains. In these studies, the protein-free polysaccharide from susceptible smooth strains of cholera and El Tor vibrios selectively inhibited type phages lysing only the S form, while similar preparations from other serological groups or from R races did not prevent phage action (White 1936).

Extensive studies on bacterial cell products with phage-adsorbing properties have been carried out with shigellae (Burnet 1934), salmonellae (Levine & Frisch 1933), staphylococci (Burnet & Lush 1935), and streptococci (Tiffany & Rakieten 1939) among others. The objectives of these investigations were to study complex cell products (Levine & Frisch 1934), the immunological relationships of bacteria (Burnet & Lush 1935), or phage specificity (Levine & Frisch 1933). The antiphage agents were polysaccharides obtained from the susceptible homologous strains but generally not present in resistant cultures derived from secondary growth or in resistant

[1] Journal Series Paper, New Jersey Agricultural Experiment Station, Rutgers University, Department of Microbiology.

These investigations were supported by a grant from the Commonwealth Fund of New York.

heterologous organisms. These substances inhibited bacteriophagia by adsorption with the virus, the effect usually being reduced or eliminated by previous exposure of the polysaccharides to antisera produced against the bacterial cells.

Effects of certain antibiotic agents on different bacterial viruses have also been studied. Penatin in the presence of glucose caused inactivation of an *E. coli* phage after an 18-hour exposure at room temperature. Although the inactivated particles retained their original morphology and were adsorbed by susceptible cells, they prevented colony formation by bacteria which the normal virus would ordinarily lyse (Anderson 1943). With streptomycin, streptothricin, clavacin, actinomycin, and penicillin it was found that a *S. aureus* phage and two *E. coli* phages were inactivated only by those agents inhibitive to gram-negative bacteria. Moreover, streptomycin-treated cells adsorbed phage whereas penicillin-treated bacteria did not (Jones 1945). Other investigations have shown that penicillin together with *S. aureus* phage K produced a more rapid killing than either agent alone; the multiplication and lytic action of the virus was not at all impaired by the antibiotic agent (Himmelweit 1945).

The object of the present investigations was to survey one group of microorganisms, namely the actinomycetes, for their ability to produce substances with antiphage properties and to isolate and study one such agent active against bacteriophages. The possibility of treating virus-infected bacteria with chemotherapeutic agents has been shown by the successful application of sodium arsenite to cells of *E. coli* after infection with phage γ. Arsenite concentrations of 7.5×10^{-5} M and over, when added to the phage–cell mixture during the latent period of intracellular virus growth, instantly inhibited virus multiplication, although they had no apparent effect upon bacterial reproduction (Spizizen 1943).

Whether microbial agents inhibitive to bacteriophagia will prove effective against animal and plant viruses remains to be determined. The fact that polysaccharides derived from *Aerobacter* sp. have been found to manifest phage-adsorptive (Ashenburg, Sandholzer, Scherp & Berry 1940) as well as plant virus-inhibitive properties (Johnson 1941) may prove to be the exception rather than the rule.

MATERIALS AND METHODS

The actinomycetes studied in the present survey have been grouped for convenience as follows: (1) cultures chosen at random from different soils, manures, composts, pond water, and from the type culture collection; (2) organisms selected at random from a soil enriched with fowl-pox virus; (3) known antibiotic producers; and (4) actinomycetes isolated from various natural substrates by use of a selective phage–agar medium (Jones & Schatz

1946). In the last group, which consisted of 29 organisms, 17 were picked because the original colonies exhibited antiphage zones; the others were isolated because of antibacterial action rather than inhibition of bacteriophagia.

Each organism was grown for 8 days in stationary culture in (1) peptone–meat extract or nutrient broth, (2) glucose-tryptone, and (3) glycerol–yeast extract media containing 0.2 per cent agar. Certain of the organisms which failed to make satisfactory growth under static conditions were cultured for 5 or 7 days in shaken flasks. The filtrates, after heat treatment at 70° C for 10 minutes, were tested by the agar tube dilution technic (Jones & Schatz 1946) with an overnight exposure period at 37° C against *E. coli* LS2 phage and *S. aureus* phage K. Any filtrates active against either or both of these phages were then tested against the *E. coli* PC phage. With the agar tube dilution procedure, the end point was that dilution of culture filtrate which produced at least a 100-fold reduction in plaque titre. Most of the active filtrates were further studied by the agar diffusion or cup method. Phage antagonism by the actinomycetes was determined by the streak test procedure.

EXPERIMENTAL RESULTS

A total of 176 strains of actinomycetes, comprising various members of the genera *Streptomyces*, *Nocardia*, and *Micromonospora*, as well as one culture of *Mycobacterium phlei*, were tested. The results indicate that 49 of these 176 actinomycetes, or 28 per cent, produced antiphage activity in filtrates from at least one of the three culture media on which each organism had been grown. Since the heat treatment used for sterilization of the culture broths may have destroyed some thermolabile active substances, it is possible that the actual number of actinomycetes which produce antiphage filtrates may exceed 28 per cent.

Table 1 presents more detailed information on the distribution of antiphage properties among the actinomycetes as determined by the agar tube dilution technic. Of 147 organisms tested on the three media, 39, or 26 per cent, were active. Only 57, or 13 per cent, of a total of 441 filtrates inhibited bacteriophagia. While most active filtrates produced a 100-fold reduction of phage titre only in a dilution of 1:2, 8 filtrates were as active at a dilution of 1:20, 2 were as active at 1:100, and one filtrate was active even at 1:200. Of the 57 active preparations, 30, or 53 per cent, inhibited the staphylococcus phage K as against 14, or 25 per cent, which were active against the *E. coli* LS2 phage. Only one filtrate was active against all three phages, while 12 inhibited two of the three phages. This selectivity of antiphage action is comparable to the selective antibacterial properties of antibiotic agents. Since only those filtrates which affected the action of the LS2 and K phages were tested against the *E. coli* PC phage, it is likely that a greater number of filtrates would have been found active if all had been tried against the PC phage.

In addition to their selective action, antibiotic and antiphage substances are similar in that the production of each is dependent to a large degree upon the composition of the medium. With antibiotics, this is well known, the specific substances required for the formation of highly active antibacterial filtrates having been designated as "activity factors" (Waksman, Schatz & Reilly 1946). Of the 39 actinomycetes reported in table 1, two were active on all three media, while 14 produced antiphage filtrates on both the tryptone-glucose and glycerol-yeast extract media. No organism was active only on the peptone–meat-extract substrate, but 9 actinomycetes were active only on the glucose and 14 only on the glycerol medium.

TABLE 1. *Antiphage properties of active culture filtrates of thirty-nine actinomycetes.*[a] Agar tube dilution technic.

Medium	End point, active filtrate dilution[b]	Number of filtrates active against only									Total active filtrates
		S3K	LS2	LS2, PC, and S3K	LS2 and LS2	PC PC	PC and PC	S3K S3K	LS2 and LS2	S3K S3K	
Peptone-meat extract	1 : 2	2	.....	.....	.....	.....	.....	.....	.....	.....	2
Glucose-tryptone	1 : 2	15	8	.....	.....	.....	2	.....	3	2	.....
	1 : 20	2	.....	.....	.....	.....	.....	2	.....	1	30
Glycerol-yeast extract	1 : 2	8	6	1	2	2	2	1	1	.....	.....
	1 : 20	2	.....	.....	.....	.....	.....	1	.....	.....	.....
	1 : 100	.....	.....	.....	.....	.....	.....	.....	2	2	.....
	1 : 200	1	.....	.....	.....	.....	.....	.....	.....	1	25
Total	.....	30	14	1	2		4		6		57

[a] Of 147 organisms tested in three different media, 39 were active.
[b] Dilution giving a 100-fold reduction in plaque titre after overnight exposure at 37° C.

Although most unheated active filtrates retained their potency when refrigerated at 4° C for three weeks, some preparations decreased in activity while others became completely inactive. Moreover, some originally active actinomycetes appeared to undergo a progressive loss of ability to produce antiphage filtrates. Studies with antibiotic agents have demonstrated similar phenomena, namely, loss of antibacterial activity in microbial filtrates and deterioration in potency of a parent culture.

That inhibition of bacteriophagia was not a pH effect was evidenced by the fact that few culture filtrates, if any, were significantly acid and that these were brought well above the critical range when mixed with the nutrient broth phage suspension. In view of the reported adsorption of phage by yeasts and molds (Rakieten, Rakieten & Doff 1936b) and the small number of active filtrates which inhibited bacteriophagia by the cup test, there is a

possibility that the phage inhibition might have been due to adsorption on spores and small mycelium fragments, some of which undoubtedly passed through the paper filters. However, the minute amount of such particles present in the clear culture filtrates as well as the dependence of antiphage action on composition of the medium would appear to eliminate this likelihood.

When tested by the agar diffusion or cup method, no active filtrates produced an appreciable antiphage zone against either of the *E. coli* phages. Of 39 filtrates which acted on the staphylococcus phage by the agar tube dilution technic, 7 produced large zones in which bacteriophagia was affected. The diameters of these zones were 33, 24, 26, 21, 17, and 35 mm. Only one of the zones contained an inner ring of antibacterial action surrounding the cup.

TABLE 2. *Antiphage and antibacterial activity of active actinomycetes.* Agar streak technic.[a]

Agar seeded with phage	Number of tests	Inhibition zones[b]			
		Antibacterial only	Antiphage only	Both antibacterial and antiphage	Absent
E. coli PC	7	2	1	3	1
E. coli LS2	11	3	6	.....	2
Staph. aureus K	35	12	6	5	12
Total	53	17	13	8	15

[a] Cultures which produced active filtrates in liquid media were streak-tested against the susceptible phages on the corresponding 1% agar media.

[b] Zones ranged from 1 to 23 mm.; antiphage zones less sharply defined and therefore less accurately measured than antibacterial zones.

All zones showed more or less complete phage inhibition except the last, in which the size rather than the number of plaques was reduced.

For the streak test, actinomycetes which produced activity in broth were tested on the corresponding agar media against those phages sensitive to the culture filtrates. The results given in table 2 reveal that in 53 such tests 17 plates showed only antibacterial zones, 13 exhibited only antiphage zones, and 8 had antibacterial areas within antiphage zones; 15 plates revealed neither type of activity. Since antibacterial action was obtained, with or without antiphage action, in 25 of the 53 tests, one might assume that in many cases the effect of the culture filtrates on bacteriophagia was due to an effect on the cells rather than on the phages by antibiotic agents present in concentrations sub-inhibitive for bacterial growth.

Of the known antibiotic-producing actinomycetes tested on the three media, *N. gardneri*, *S. antibioticus*, and *S. lavendulae* failed to exhibit antiphage properties, although certain filtrates were antibacterial. On the other hand, some streptomycin-producing strains of *S. griseus* as well as an asporo-

genous inactive variant (Schatz & Waksman 1945) were found to yield culture filtrates highly active against phage. Other sporogenous strains, No. 42.1 and 3326a, did not exhibit antiphage action, although the former produced streptomycin while the latter did not (table 3). Moreover, a strain such as No. 19 produced antibacterial but not antiphage activity in certain media while the reverse was true with other substrates. These results together with the observation that different preparations of streptomycin varied in their activity upon *E. coli* PC phage (Jones 1945) indicated that the antiphage effect of certain streptomycin lots might be due to some substance other than the antibacterial agent itself.

TABLE 3. *Activity of different strains of S. griseus against bacteria and S. aureus phage K.*

Agar tube dilution test. 15-day culture filtrates.

S. griseus strain	Medium[a]	*E. coli* units per ml., cup test	Phage survival at filtrate dilution[b]			
			1 : 2	1 : 20	1 : 100	1 : 200
19 (sporogenous)	DA	0	++++	++++	++++	++++
	TG	14	AB	+++	++++	++++
	YG	0	+	+	++	++
	GN	16	AB	+++	++++	++++
42.1 (sporogenous)	DA	0	++++	++++	++++	++++
	TG	23	AB	++++	++++	++++
	YG	40	AB	++	++++	++++
	GN	45	AB	++	++++	++++
Variant 3 (asporogenous)	DA	0	++++	++++	++++	++++
	TG	0	+	++	++	++
	YG	0	+	++	++	+++
	GN	0		+	+	+
3326a (sporogenous)	TG	0	++++	++++	++++	++++
	YG	0	++++	++++	++++	++++
	GN	0	++++	++++	++++	++++

[a] DA = dextrose asparagin; TG = tryptone-glucose; YG = yeast extract-glycerol; GN = glucose-nutrient broth. All media contained 0.2% agar.

[b] AB = antibacterial action; ++++ = normal plaque titre; ++ = a 10-fold reduction in plaque titre; + = a 100-fold reduction or more in plaque titre.

Comparisons were, therefore, made of the antiphage and antibacterial properties of several lots of streptomycin which differed considerably in potency. These were dissolved in nutrient broth and neutralized, and the resulting solutions were sterilized by heating at 75° C for 10 minutes before being tested against *S. aureus* phage K. Approximately 1,500 μg. of streptomycin contained in 1.5 ml. were mixed with an equal volume of phage suspension of such titre that plaque counts of surviving phage were made at dilutions where antibacterial activity was eliminated. As shown in table 4, the hydrochloride lots were characterized by considerably greater antiphage action than the formate samples, although the antibacterial activity per ml., as determined by cup assay, was about the same throughout.

The difference between the two streptomycin salts suggested that the formate ion per se might affect antiphage action or that the formate preparations might contain some other factor which inhibited the phage-inactivating agent. The former possibility was eliminated by the observation that a solution of streptomycin hydrochloride (300 μg./ml.) to which 1.7 mg. sodium formate per ml. had been added retained its antiphage activity when tested after incubation overnight at 37° C.

On the other hand, a formate salt of streptomycin was found definitely to interfere with the phage-inactivating ability of one of the hydrochloride preparations. For this experiment, phage was exposed to the hydrochloride, formate, and a mixture of the two in which 50 per cent of the antibacterial activity was contributed by each preparation. The results revealed that 510

TABLE 4. *Activity of different streptomycin preparations against S. aureus phage K.*

Streptomycin preparation	*E. coli* units per mg.[a]	Phage exposed to units per ml.[a]	Surviving phage, particles per ml.
Formate	19	520	27×10^5
Formate	45	500	14×10^5
Formate	58	500	50×10^4
Formate	110	480	10×10^5
Hydrochloride[b]	100	510	21×10^2
Hydrochloride[b]	400	450	35×10^2
Nutrient broth control	0	0	15×10^8

[a] Cup assay.
[b] Obtained through the courtesy of Merck and Co., Inc., Rahway, N. J.

μg. per ml. of the hydrochloride alone caused approximately a 10,000-fold reduction in phage titre. On the other hand, when phage was exposed to 1000 μg. per ml. of the formate-hydrochloride mixture, in which both preparations were equally present on the basis of antibacterial unitage, the titre was decreased only about 10-fold. This same order of activity was found with 500 μg. per ml. of the formate alone.

Since the hydrochloride lots were obtained from Merck & Co., Inc., while the formate samples were prepared in our own laboratory, it is difficult to interpret the data because the two types of products very probably differed in respect to strain of *S. griseus*, composition of medium, conditions of growth, and method of recovery of streptomycin. However, the fact that an antiphage agent is obtained with strains which do not produce streptomycin as well as with streptomycin-producing strains in media where no antibacterial substance is formed (table 3) indicates that the antiphage action is due to a product of *S. griseus*. This substance cannot be isolated by the charcoal adsorption acid-alcohol elution technic used to recover streptomycin. It differs from the second antibiotic agent isolated from *S. griseus* (Waksman,

Schatz & Reilly 1946), since an active preparation of this lipid-like substance has been found to lack activity against bacteriophage.

For detailed study, *Streptomyces* No. 193 was chosen because it produced filtrates highly active against the *E. coli* PC and *S. aureus* bacteriophages, although the same filtrates possessed no antibacterial properties when tested by the agar dilution method against *E. coli*, *S. aureus*, *B. subtilis*, and *B. mycoides*. The parent culture, which had been isolated from a fowl-pox-enriched soil, underwent marked variation. The original organism upon serial transfer repeatedly grew in distinct areas of white and mouse-gray on dextrose-asparagin agar slants. By plating out and single colony selection, a pure white and a mouse-gray, or brown, strain were obtained. Both of these

TABLE 5. *Antiphage activity of culture filtrates of Streptomyces sp. No. 193 in different liquid media.*

Agar tube dilution test

Medium[a]	Phage survival at filtrate dilutions[b]					
	S. aureus phage K			*E. coli* PC phage		
	1 : 2	1 : 20	1 : 200	1 : 2	1 : 20	1 : 200
Peptone-meat extract	+	+	++++	+	+++	++++
Peptone-meat extract-glucose	+	+	++++	.....	.....	.....
Peptone-glucose	.....	+	++++	.....	.....	.....
Tryptone-starch	0	0	++	0	+	+++
Yeast extract-glycerol	.....	+++	++++	.....	.....	.....
Sodium nitrate-glucose-corn steep liquor	.....	+	+++	.....	.....	.....
Glutamic acid-glucose	.....	+	+	.....	.....	.....
Yeast extract-glucose-casein	.....	++++	++++	.....	.....	.....

[a] Mineral salts plus 0.2% agar in each medium.

[b] 9-day-old culture filtrates tested. ++++ = no plaque reduction; ++ = a 10-fold reduction in plaque titre; + = a 100-fold reduction in plaque titre; 0 = no viable phage, complete inactivation.

were stable and active with about the same antiphage spectra; both produced culture filtrates devoid of antibacterial action. In addition to these strains, a sporulating variant with a purple reverse, a black sporogenous variant, and an asporogenous, nocardial form were obtained. Of these three types, which were stable upon transfer, the first was found to be inactive against bacteriophages and bacteria; the last two were not tested. Variations similar to these have been observed with the actinomycetes that produce streptothricin and streptomycin (Schatz & Waksman 1945; Waksman & Schatz 1945).

In determining the activity of No. 193 in different media, antiphage action was obtained with several substrates, as illustrated in table 5. However, only the glucose-tryptone and glucose-glutamic acid media were used. In stationary cultures, the actinomyces produced filtrates which by the agar tube dilution method gave a 100-fold reduction of phage titre at dilutions of 1 : 20 to 1 : 100, the end-point varying with different lots. The active agent

could be concentrated from the culture filtrate by adsorption on charcoal and subsequent elution with a 1:1 mixture of ether and 95 per cent ethyl alcohol, although the percentage of recovery was rather low. The antiphage substance does not decrease in activity if heated for 10 minutes at 70–80° C. However, Seitz filtration causes some loss in potency. Considerably greater activity was obtained by extraction of moist 9-day-old pellicles with ether-alcohol. Upon removal of the organic solvents, the residue formed a stable aqueous suspension. Some such preparations by the agar tube test produced 100-fold reductions in plaque titre of *S. aureus* phage K at dilutions of about 1:200,000. On a dry weight basis this represented dilutions of approximately 1:1,000,000.

It appears that the antiphage agent acted directly upon the phage particles rather than through an effect on the host cells, since it was found that a pre-exposure of phage to agent was required and that the degree of inactivation for a given phage titre varied within limits with the concentration of the agent. The fact that untreated phage produced normal lysis when plaque-counted with semisolid agar to which the agent had been added immediately before plating indicates that once a phage particle is adsorbed on or has entered into a host cell, the antiphage agent can not inhibit its multiplication and subsequent lytic effect.

When tested against fowl pox virus, the 193 concentrate was active in vitro but not in vivo. With 11-day-old chick embryos, it was found that the agent, undiluted as well as diluted 1:20, completely inactivated the virus after overnight exposure at room temperature. However, no protective effect was obtained when infected eggs were treated with the agent or when virus and agent were injected simultaneously but separately.

SUMMARY AND CONCLUSIONS

The antagonistic action of certain microorganisms upon bacteriophages and the inhibitive effects of substances of microbial origin upon bacteriophagia are well known. The present study concerns phage antagonism by actinomycetes and the production of an antiphage agent by a representative of this group of microorganisms.

Of 176 actinomycetes isolated by different means from a variety of substrates and grown in three media, 28 per cent gave culture filtrates active against one or more of three phages when tested by the agar tube dilution technique. Antiphage activity depended upon composition of the culture medium and was selective in nature. Both of these aspects are well known with antibiotic agents. Of the cultures which produced antiphage filtrates by the agar tube test, not all were active by the streak test. Some were only antibacterial; others were only antiphage. Certain organisms exhibited an antibacterial within an antiphage zone; several actinomycetes lacked either

type of action. Of the culture filtrates active by the agar tube dilution method, several produced zones of phage inhibition only against the staphylococcus bacteriophage when cup-tested.

Of the known antibiotic-producing actinomycetes, only *S. griseus* produced antiphage filtrates. The active agent was not streptomycin, since it was obtained with strains which did not produce this antibiotic as well as with streptomycin-producing strains cultured in certain media where no antibacterial substance was formed. Therefore, the nocardia-like variant and certain related streptomyces strains which have been found to differ on the basis of their capacity to produce streptomycin cannot be separated by their ability to produce the antiphage agent.

While two samples of streptomycin-hydrochloride were active against phage, four formate preparations were not. Moreover, the impure streptomycin-formate contained some substance which antagonized the antiphage action of the hydrochloride.

One active species of *Streptomyces*, isolated from a soil enriched with fowl-pox virus, was studied in detail. This organism produced in several media a thermostable antiphage agent active against *S. aureus* phage K and *E. coli* PC phage, but not against *E. coli* LS2 phage. The substance could be concentrated by adsorption on charcoal and subsequent elution with ether-alcohol, although considerably greater activity was obtained by ether-alcohol extraction of the mycelium of the organism. The agent formed a stable aqueous suspension which inhibited the staphylococcus bacteriophage at a dilution of about 1:1,000,000 on a dry weight basis. From the experimental results, it is believed that the effect of the antiphage agent is on the phage particles themselves rather than on the host cells, and that once infection has taken place the agent does not interfere with phage multiplication.

The 193 concentrate inactivated fowl-pox virus in vitro but was ineffective in vivo.

ACKNOWLEDGMENT

The authors wish to express their appreciation to Dr. Selman A. Waksman for his advice and many valuable suggestions during the course of these investigations.

NEW JERSEY AGRICULTURAL EXPERIMENT STATION,
RUTGERS UNIVERSITY
NEW BRUNSWICK, NEW JERSEY

Literature Cited

Anderson, T. F. 1943. The action of an antibiotic substance (penatin) on bacteriophage. Jour. Bact. **46**: 110.

Ashenburg, N. J., Sandholzer, L. A., Scherp, H. W. & Berry, G. P. 1940. The influence of bacterial and non-bacterial polysaccharides upon bacteriophage. Jour. Bact. **39**: 71–72.

Burnet, F. M. 1934. The phage-inactivating agent of bacterial extracts. Jour. Path. Bact. **38**: 285–299.

Burnet, F. M. & Lush, D. 1935. The staphylococcal bacteriophages. Jour. Path. Bact. **40**: 455–469.

Himmelweit, F. 1945. Combined action of penicillin and bacteriophage upon staphylococci. Lancet **249**: 104–105.

Johnson, J. 1941. Chemical inactivation and the reactivation of a plant virus. Phytopathology **31**: 679–701.

Jones, D. 1945. The effect of antibiotic substances upon bacteriophage. Jour. Bact. **50**: 341–348.

Jones, D. & Schatz, A. 1946. Methods of study of antiphage agents produced by microorganisms. Jour. Bact. **51**: 566.

Levine, P. & Frisch, A. W. 1933. Further observations on specific inhibition of bacteriophage action. Proc. Soc. Exp. Biol. Med. **31**: 46–48.

———— & ————. 1934. Observations on phage inhibition by bacillary extracts. Proc. Soc. Exp. Biol. Med. **32**: 341–343.

Levine, P., Frisch, A. W. & Cohen, E. V. 1934. On absorption of phage by bacilli. Jour. Immunol. **26**: 321–327.

Rakieten, M. L. 1942. A consideration of factors involved in the preparation and therapeutic use of bacteriophage. Military Surgeon **91**: 151–157.

————. 1932. Studies with staphylococcus bacteriophage. 1. The preparation of polyvalent staphylococcus bacteriophage. Yale Jour. Biol. Med. **4**: 807–818.

Rakieten, M. L., Rakieten, T. L. & Doff, S. 1936a. Inhibition of staphylococcus bacteriophage and the virus of vesicular stomatitis. Jour. Bact. **31**: 55–56.

————, ———— & ————. 1936b. The adsorption of staphylococcus bacteriophages. Jour. Bact. **32**: 505–518.

Schatz, A. & Waksman, S. A. 1945. Strain specificity and production of antibiotic substances IV. Variation among actinomycetes with special reference to *Actinomyces griseus*. Proc. Nat. Acad. **31**: 129–137.

Spizizen, J. 1943. Some preliminary studies on the mechanism of virus multiplication. Proc. Nat. Acad. **29**: 109–114.

Tiffany, E. J. & Rakieten, M. L. 1939. The absorption of bacteriophage by sensitized enterococci. Jour. Bact. **37**: 333–350.

Waksman, S. A. & Schatz, A. 1945. Strain specificity and production of antibiotic substances. VI. Strain variation and production of streptothricin by *Actinomyces lavendulae*. Proc. Nat. Acad. **31**: 208–214.

Waksman, S. A., Schatz, A. & Reilly, H. C. 1946. Metabolism and chemical nature of *Streptomyces griseus*. Jour. Bact. **51**: 753–759.

White, P. B. 1936. Differential fixation of cholera phages by extracts of *V. cholerae*. Jour. Path. Bact. **43**: 591–593.

Williams, C. H., Sandholzer, L. A. & Berry, G. W. 1940. The inhibition of bacteriophagy by cholesterol and by bacterial and non-bacterial phospholipids. Jour. Bact. **40**: 517–527.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 1, PP. 20–37 JANUARY, 1947

THE ROLE OF CERTAIN ENVIRONMENTAL FACTORS IN GROWTH AND REPRODUCTION OF PROTOSIPHON BOTRYOIDES KLEBS—II. VEGETATIVE GROWTH[1]

SISTER M. LAURENCE MAHER, I.H.M.

INFLUENCE OF ILLUMINATION

Two series of experiments were set up to determine the effect on growth of *Protosiphon* of different lighting periods. Six flasks of 0.06 per cent Bristol's solution and six tube slants with the same solution in 1.5 per cent agar and inoculated with clone 8*B*2 were used for each experiment in one series and the same medium with the addition of 0.25 per cent glucose was used for the second series. One set of six slants and six flasks with inorganic medium and a similar set containing glucose were kept in total darkness for three months. Additional sets with and without glucose were kept in light-tight boxes except during daily lighting periods of four, eight, ten, twelve, and twenty-four hours.

The longest sacs were produced on slants that were exposed to a ten-hour period of daily illumination. In every case the mean length of one hundred sacs and the amount of centrifugate per flask was greater in the glucose-containing medium. In all cases too the total amount of centrifugate increased with the length of the period of daily illumination. From flasks with inorganic liquid medium, three times as much material was centrifuged from flasks grown under twenty-four hours daily illumination as from flasks with a four-hour lighting period. In the corresponding series containing 0.25 per cent glucose, the amount of centrifugate was four times as great from flasks lighted twenty-four hours as from those with four hours of light daily.

There was a thin layer of growth, green in color and macroscopically visible, on slants with inorganic medium that were kept in total darkness for three months. Microscopic examination showed that the growth consisted of small spherical cells and numerous zygotes. The results indicate that very small amounts of nutrient material are sufficient to sustain growth of *Protosiphon* for three months. These were probably introduced with the inoculum or available as impurities in the agar (Robbins 1939). On the slants with 0.25 per cent glucose added to the inorganic medium, there was a thick layer of red coenocysts. In the flasks containing glucose medium, there was a thick layer of red coenocysts also macroscopically visible. The experiment indicates that considerable growth may occur in darkness when carbohydrate is sup-

[1] Part I of this series appeared in Bull. Torrey Club 73: 000–000. Numbering of illustrations is continuous throughout the series. A list of literature cited will appear in part III.

plied. It also shows that light is not requisite for formation of red coenocysts, and, inasmuch as zygotes were present in all the cultures, that conjugation takes place readily in darkness.

INFLUENCE OF THE CULTURE MEDIUM—PHYSICAL FACTORS

A. Salt Concentration of the Medium. Klebs (1896), Livingston (1900, 1901, 1905), Artari (1904, 1906), Pringsheim (1914, 1926a) and others have demonstrated that the concentration of the solution in which *Protosiphon* and other organisms are cultured has a decided effect on their growth and reproduction. In order to obtain information on the optimum concentration of culture media for the growth of clonal cultures, growth was observed in a number of different culture media of varying concentrations. The first five media used in table 6 are listed by Bold (1942). Slight changes, such as the addition of minor elements, were made, and the formulae are listed here as they were used in the experiments.

Beyerinck's Solution, 1898

Distilled H_2O	100.0 ml.	1% $FeCl_3$ solution	2 drops per liter
NH_4NO_3	0.05 gram	minor elements solution	2 ml. per liter
K_2HPO_4	0.02 gram	molybdic acid solution	1 ml. per liter
$MgSO_4 \cdot 7H_2O$	0.02 gram		
$CaCl_2 \cdot 2H_2O$	0.01 gram		

= 0.1% solution by weight

Bristol's Solution, 1919

KH_2PO_4	0.7 gram	Distilled H_2O	1000.0 cc.
K_2HPO_4	0.3 gram	1% $FeCl_3$ solution	4 drops
$NaNO_3$	1.0 gram	minor elements solution	2 ml.
$CaCl_2$	0.1 gram	molybdic acid solution	1 ml.
$MgSO_4$	0.3 gram		
NaCl	0.1 gram		

= 0.25% solution by weight

Detmer's Solution, 1888

$Ca(NO_3)_2$	1.0 gram	Distilled H_2O	1000.0 ml.
KCl	0.25 gram	1% $FeCl_3$ solution	3 drops
$MgSO_4$	0.25 gram	minor elements solution	1.5 ml.
KH_2PO_4	0.25 gram	molybdic acid solution	0.75 ml.

= 0.175% solution by weight

Knop's Solution, 1865 (from Bold, 1942)

Part A		Part B	
$Ca(NO_3)_2$	4.0 gram	KNO_3	1.0 gram
Distilled H_2O	500.0 ml.	KH_2PO_4	1.0 gram
1% $FeCl_3$ solution	3 drops	$MgSO_4 \cdot 7H_2O$	1.0 gram
minor elements solution	2 ml.	Distilled H_2O	500.0 ml.
molybdic acid solution	1 ml.		

= 0.7% solution by weight

Lefévre's Solution, 1937

KNO_3	0.2 gram	Distilled H_2O	1000.0 ml.
K_2HPO_4	0.4 gram	1% $FeCl_3$ solution	2 drops
$MgSO_4$	0.25 gram	minor elements solution	1 ml.
$Ca(NO_3)_2$	0.25 gram	molybdic acid solution	0.5 ml.

= 0.11% solution by weight

Pringsheim's Solution, 1926a

KNO_3	0.1 %	The following were added to each liter of solution:	
$MgSO_4 \cdot 7H_2O$	0.01%		
$(NH_4)_2HPO_4$	0.02%	1% $FeCl_3$ solution	2 drops
$CaSO_4$	0.01%	minor elements solution	1 ml.
		molybdic acid solution	0.5 ml.

= 0.14% solution by weight

Minor elements stock solution
Craig and Trelease, 1937

$ZnSO_4 \cdot 7H_2O$	100 mgm.	$CuSO_4 \cdot 5H_2O$	3 mgm.
H_3BO_3	100 mgm.	Distilled H_2O	1000.0 ml.
$MnSO_4 \cdot 4H_2O$	150 mgm.		

Molybdic acid solution

85% molybdic acid	3 mgm.
Distilled H_2O	1000.0 ml.

Four concentrations of each solution were inoculated with clone 8*B*2. Six flasks each containing 35 ml. of solution were used for each concentration and the cultures were permitted to grow for fifty days. The results are summarized in table 6.

In the experiments with liquid media, the amount of centrifugate per flask is a better criterion of the amount of growth than the length of sacs. Some media tend to stimulate repeated gamete formation and in such cases no long sacs develop. In table 6, the longest sacs were found in 0.1 per cent Beyerinck's solution, but the total amount of material centrifuged from flasks with this medium was less than the total from any other medium except Pringsheim's.

The largest amount of material was centrifuged from the flasks with Bristol's solution. Detmer's solution gave the next largest yield and the sacs were a little larger than those in Bristol's solution. The pH of Bristol's solution changed less than that of any of the solutions used and this is probably the most important advantage in its use. The pH of Detmer's solution at the beginning of the experiment was lower than that of a freshly prepared solution because it had been standing. There was no significant difference in size of the sacs in any of the concentrations of Detmer's solution, but the highest concentration used was 0.175 per cent. The higher concentrations of Bristol's solution (0.25%) and Knop's solutions (0.7%) increase the possibility of

osmotic effects (Livingston 1900). The final hydrogen-ion concentration of the more dilute concentrations of Beyerinck's solution was high and the red color of the coenocysts present was visible to the naked eye.

TABLE 6. *Influence of the concentration of the medium on growth at an average temperature of 16.5° C of clone 8B2.*
(In all experiments except where otherwise noted the pH was determined by means of a glass electrode.)

Solution	Per cent conc. by weight of solution	pH		Color intensity	Amount centrifuged from one flask (ml.)	Mean length of 100 cells after 50 days (mm.)
		At beginning of experiment	After 50 days			
Beyerinck's 1898	0.10	7.0	5.3	2	0.05	0.52
	0.05	6.8	3.8	1	0.02	0.13
	0.025	6.5	3.7	1	0.03	0.05
	0.0125	6.2	3.7	0	0.01	0.04
Bristol's 1919	0.25	6.2	6.2	2+	0.07	0.13
	0.125	6.3	6.4	2	0.06	0.12
	0.06	6.3	6.5	2	0.06	0.20
	0.03	6.3	6.6	2	0.04	0.20
Detmer's 1888	0.175	4.5	5.7	2	0.05	0.23
	0.08	4.2	6.3	2	0.06	0.20
	0.04	4.0	6.3	2	0.05	0.25
	0.02	4.0	6.8	2	0.06	0.25
Knop's 1865	0.70	3.9	4.0	0	0.01	0.03
	0.35	4.3	5.1	1	0.04	0.12
	0.175	4.6	5.8	2	0.05	0.12
	0.09	4.4	6.0	2	0.07	0.15
Lefévre's 1937	0.11	7.4	7.0	2	0.05	0.07
	0.055	7.4	7.2	2	0.05	0.17
	0.03	7.2	7.8	1+	0.05	0.06
	0.015	6.9	7.2	1	0.03	0.08
Pringsheim's 1926a	0.14	6.8	6.2	1−	0.01	0.03
	0.07	6.8	4.4	1	0.04	0.12
	0.035	6.8	5.5	1	0.03	0.12
	0.018	6.7	4.8	1−	0.01	0.06

B. Concentration of Agar. Moewus (1933) reports that concentrations of 0.7–1.0 per cent agar evoke the production of large sacs in *Protosiphon*, while higher concentrations are inhibiting in this respect. Pringsheim's and Bristol's solutions were selected for testing the effect of agar concentration on the growth of *Protosiphon* because good results had been secured with them in other experiments. Table 7 and figure 18 list the agar concentrations used and the mean length of sacs for the different observation periods. At the end of twelve days, the longest sacs in both solutions were produced on agar in 0.75 per cent concentration, while the size decreased markedly in lower and higher concentrations.

At the end of twenty-four days, the longest sacs occurred in 0.5 per cent agar in Bristol's solution and on 0.75 per cent agar in Pringsheim's solution.

Sacs from 0.06 per cent Bristol's solution without agar were mostly spherical (fig. 22). The mean lengths of sacs from either 0.5 per cent or 0.75 per cent agar (fig. 23) were approximately six times as great as the mean length of sacs from 4.5 per cent agar concentration (fig. 24). Sacs from 2.5 per cent agar were more than three and one-half times as long as those from 4.5 per cent agar concentration.

The mean lengths of sacs were not as great when Pringsheim's solution was used, but the form of the curve in figure 18 indicates the effects of agar concentration were essentially the same with the two media. On Pringsheim's solution, the longest sacs at the ends of both the twelve- and the twenty-four-

TABLE 7. *Effect of agar concentration on cell size of clone 8B2 cultures at an average temperature of 17° C in 0.06 per cent Bristol's and 0.06 per cent Pringsheim's solutions.*

Agar conc. (per cent)	Mean length of 100 sacs in mm. after					
	12 days	24 days	40 days	12 days	24 days	40 days
	0.06 per cent Bristol's solution			0.06 per cent Pringsheim's solution		
0.0	0.04	0.09	0.14	0.05	0.06	0.20
0.25	0.05	0.20	.....	0.10	0.15	0.60
0.5	0.55	**0.94**	0.5	0.19	0.25	0.75
0.75	**0.6**	0.88	.....	**0.30**	**0.75**	**1.00**
1.0	0.45	0.77	0.87	0.20	0.55	**1.00**
1.5	0.27	0.75	**1.30**	0.15	0.40	**1.00**
2.0	0.25	0.75	0.87	0.17	0.40	0.88
2.5	0.20	0.55	0.75	0.17	0.25	0.65
3.0	0.10	0.44	0.75	0.15	0.21	0.37
3.5	0.03	0.19	0.75	0.15	0.20	0.25
4.0	0.05	0.12	0.75	0.06	0.12	0.23
4.5	0.03	0.15	0.60	0.03	0.12	0.20
5.0	0.03	0.12	0.45	0.04	0.12	0.21

day periods were on the slants with 0.75 per cent agar. Sacs with two or more lobes separated by septa were common in cultures with less than 1 per cent agar. In 0.06 per cent Pringsheim's solution in liquid form, most cells were spherical just as they were in Bristol's solution in liquid form. After twenty-four days growth on agar concentrations higher than 0.75 per cent, the mean lengths of the sacs were less than on 0.75 per cent, but the diameter of the aerial portions was greater (figs. 25–26).

These observations for a growth period of twenty-four days support Moewus' observation (1933) that lower concentrations of agar effect increased cell size, apparently by stimulating increased growth of the rhizoidal portion of the cell. This is probably related to thigmotropic or geotropic stimuli. Higher concentrations of agar retard growth initially, but this effect is overcome to some extent in older cultures. For general use however, cultures inoculated on agar concentrations of 0.5 or 0.75 per cent are difficult to handle because the agar breaks so easily. With 1 or 2 per cent agar, the dishes can be moved around without undue disturbance of the culture.

After forty days, the plants in Bristol's solution in agar concentrations of 3–5 per cent were still in vegetative condition and growing. The largest sacs were on slants solidified with 1.5 per cent agar. On agar concentrations below 2 per cent, the contents of most of the sacs had formed coenocysts. No figure is recorded in table 7 for the mean length of sacs from cultures with 0.25 per cent agar or 0.75 per cent agar added to Bristol's solution and allowed to grow for forty days, because only small coenocysts were observed in these cultures. The larger sacs in these cultures evidently were stimulated to swarmer formation after the twenty-four-day observations were made.

On Pringsheim's solution, sacs were equally long after 40 days on 0.75 per cent, 1.0 per cent, and 1.5 per cent agar. On concentrations of agar of 3.5–5 per cent there was a significant increase in length of sacs between the 24- and 40-day growth periods. Most of the sacs in all the cultures in Pringsheim's solution were in vegetative condition and therefore still growing.

INFLUENCE OF THE CULTURE MEDIUM—CHEMICAL FACTORS

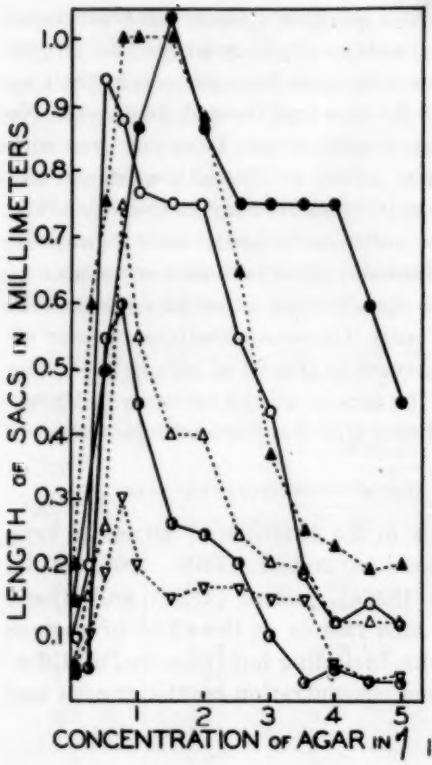
The role of various chemical elements in the nutrition of algae has been extensively investigated by such workers as Artari (1904, 1906, 1913), Chodat (1913), Pringsheim (1912, 1914, 1926a), Luksch (1932), and others.

The present report deals only with such factors as the effect of various culture media, the effect of minor elements, including molybdenum, of different nitrogen sources, and of hydrogen-ion concentration on the growth and reproduction of *Protosiphon*.

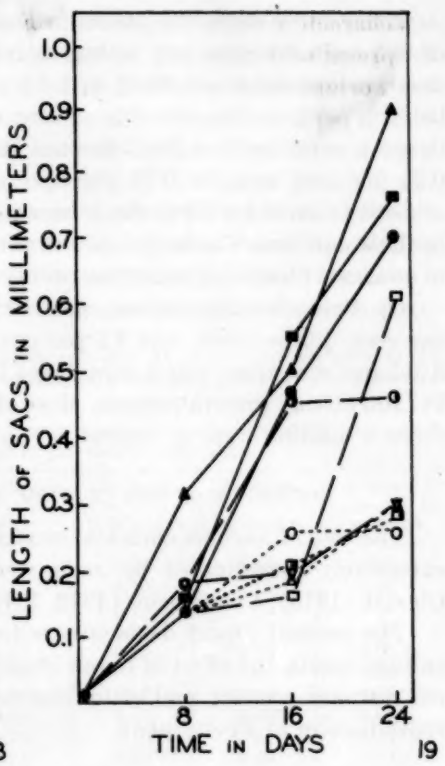
A. Inorganic media

1. Experiments with Various Media. Beyerinck's, Bristol's, Detmer's, Lefévre's, and Knop's solutions (p. 21, 22) were prepared in concentrations of 0.06 per cent by weight. The hydrogen-ion concentration of Knop's and of Detmer's solutions was adjusted to pH 6.0 by adding N KOH. The solutions were then resterilized. From each medium, six slants solidified with 1.5 per cent agar and six flasks each containing 35 ml. of liquid medium were inoculated with clone 2*B*1 and grown for 24 days at an average temperature of 20° C.

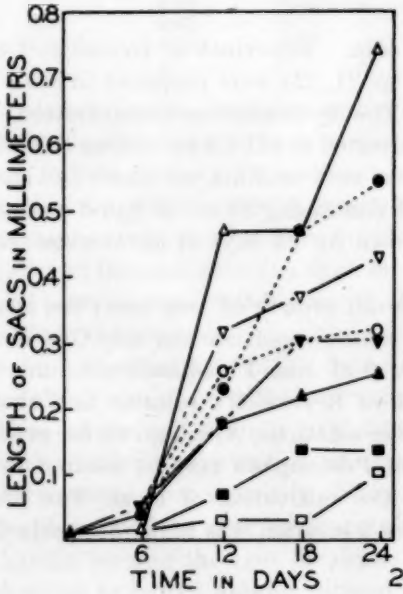
The temperature was too high to permit growth of long sacs; the mean length of sacs on slants made from Beyerinck's solution was only 0.04 mm., and on the other media approximately 0.20 mm. Five-hundredths ml. of centrifugate were obtained from a flask of Beyerinck's solution and about 0.03 ml. from a flask with each of the other solutions. Although rather crude, these data indicate that good growth of *Protosiphon* may be secured in a number of media commonly used for the cultivation of algae. The final hydrogen-ion concentration of Beyerinck's solution was high (see table 6).


LENGTH OF SACS IN MILLIMETERS
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
1
2
3
4
5
CONCENTRATION OF AGAR IN %

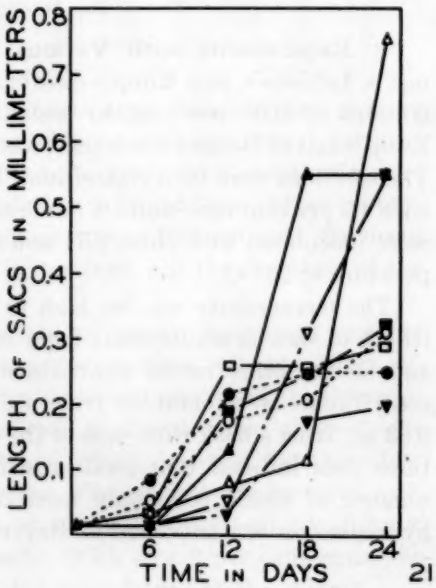
18


LENGTH OF SACS IN MILLIMETERS
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
8
16
24
TIME IN DAYS

19


LENGTH OF SACS IN MILLIMETERS
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
6
12
18
24
TIME IN DAYS

20


LENGTH OF SACS IN MILLIMETERS
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
6
12
18
24
TIME IN DAYS

21

This characteristic makes the solution less desirable for use. The same objection prevails for Detmer's and Knop's solutions if they are made according to the original formulae.

2. Experiments on the Form of Nitrogen Required. The increase in hydrogen-ion concentration of Beyerinck's solution indicates that ammonium nitrogen is being utilized. In an attempt to determine the effect of different nitrogen sources on the growth of *Protosiphon* and on the hydrogen-ion concentration of the solutions, Detmer's, Bristol's, and Pringsheim's solutions were prepared with NO_3/NH_4 ionic ratios of 100/0, 50/50, and 0/100. The total nitrogen concentrations and the weight of salts used was kept approximately unchanged for each solution. The different NO_3/NH_4 ratios were obtained by varying the proportions of salts containing nitrogen as follows.

Explanation of figures 18–21

FIG 18. Graph showing the effect on length of sacs in clone 8*B*2 of different concentrations of agar used to solidify 0.06% concentrations of Bristol's and of Pringsheim's solutions.

- length of sacs after 12 days in 0.06% Bristol's solution.
- length of sacs after 24 days in 0.06% Bristol's solution.
- length of sacs after 40 days in 0.06% Bristol's solution.
- length of sacs after 12 days in 0.06% Pringsheim's solution.
- length of sacs after 24 days in 0.06% Pringsheim's solution.
- length of sacs after 40 days in 0.06% Pringsheim's solution.

FIG. 19. Effect of different NO_3/NH_4 ionic ratios with 0.06% concentrations of various media on the growth of clone 8*B*2 on slants with 1.5% agar at a temperature of 17.5° C.

Solution	Ionic ratio	Solution	Ionic ratio
Bristol's	100/0	Bristol's	0/100
Detmer's	100/0	Detmer's	0/100
Pringsheim's	100/0	Pringsheim's	0/100
Bristol's	50/50		
Detmer's	50/50		
Pringsheim's	50/50		

FIG. 20. Effect of 0.25% and 0.5% concentrations of various carbohydrates added to 0.06% Bristol's solution solidified with 1½% agar on the growth of clone 2*B*1 at a temperature of 20½° C.

- 0.25% dextrose
- 0.5% dextrose
- 0.25% inulin
- 0.5% inulin
- 0.25% sucrose
- 0.5% sucrose
- 0.25% xylose
- 0.5% xylose

FIG. 21. Effect of addition of 0.25% and 0.5% concentrations of fructose, maltose, mannose and raffinose to 0.06% Bristol's solution with 1.5% agar on the length of sacs of clone 2*B*1 at a temperature of 20° C.

- 0.25% fructose
- 0.5% fructose
- 0.25% maltose
- 0.5% maltose
- 0.25% mannose
- 0.5% mannose
- 0.25% raffinose
- 0.5% raffinose

Bristol's Solution

Four drops of 1% aqueous solution of $FeCl_3$, 2 ml. of minor elements solution (Craig and Trelease, 1937) and 1 ml. of molybdic acid solution were added to each liter of the undiluted solution. Other salts employed were:

NO_3/NH_4 ionic ratio of 100/0

KH_2PO_4	1.0 gram	$MgSO_4$	0.3 gram
$NaNO_3$	1.0 gram	NaCl	0.1 gram
$CaCl_2$	0.1 gram	Distilled H_2O	1000.0 ml.

Total = 0.25% solution by weight

NO_3/NH_4 ionic ratio of 50/50

KH_2PO_4	1.0 gram	$CaCl_2$	0.1 gram
Na_2PO_4	0.4 gram	$MgSO_4$	0.3 gram
NH_4NO_3	0.5 gram	NaCl	0.1 gram
Distilled H_2O	1000.0 ml.		

Total = 0.24% solution by weight

NO_3/NH_4 ionic ratio of 0/100

KH_2PO_4	1.0 gram	$(NH_4)_2SO_4$	0.75 gram
K_2HPO_4	0.2 gram	$MgSO_4$	0.3 gram
$CaCl_2$	0.1 gram	NaCl	0.1 gram

Total = 0.25% solution by weight

One liter of solution in each case contained 0.16 gram nitrogen. Three volumes of distilled water were added to one volume of solution for use. This gave a concentration of 0.06 per cent by weight with 0.004 per cent by weight of nitrogen.

Detmer's Solution

Three drops of 1 per cent aqueous solution of $FeCl_3$, 2 ml. of minor elements solution and 1 ml. of molybdic acid solution were added to a liter of the undiluted solution. The other salts are listed below.

NO_3/NH_4 ionic ratio of 100/0

$Ca(NO_3)_2$	1.0 gram	KH_2PO_4	0.25 gram
KCl	0.25 gram	Distilled H_2O	1000.0 ml.
$MgSO_4$	0.25 gram		

Total = 0.18% solution by weight

NO_3/NH_4 ionic ratio of 50/50

KH_2PO_4	0.25 gram	$(NH_4)_2SO_4$	0.4 gram
K_2HPO_4	0.15 gram	KCl	0.25 gram
$Ca(NO_3)_2$	0.5 gram	$MgSO_4$	0.25 gram
Distilled H_2O	1000.0 ml.		

Total = 0.18% solution by weight

NO_3/NH_4 ionic ratio of 0/100

KH_2PO_4	0.35 gram	$CaCl_2$	0.1 gram
K_2HPO_4	0.2 gram	KCl	0.25 gram
$(NH_4)_2SO_4$	0.6 gram	$MgSO_4$	0.25 gram
Distilled H_2O	1000.0 ml.		

Total = 0.18% solution by weight

One liter of either of the first two of these solutions contains 0.17 gram of nitrogen. The formula with a NO_3/NH_4 ionic ratio of 0/100 contains 0.13 gram per liter of nitrogen. For use two volumes of distilled water were added to one volume of solution. The culture medium then had a salt concentration of approximately 0.06 per cent by weight of which 0.006 per cent in the first two and 0.004 per cent in the third solution consisted of nitrogen.

Pringsheim's Solution

Two drops of 1 per cent aqueous solution of $FeCl_3$, 2 ml. of minor elements solution and 1 ml. of molybdic acid solution were added to a liter of undiluted solution. The composition of the solutions with the different ionic ratios follows:

NO_3/NH_4 ionic ratio of 100/0

KNO_3	1.0 gram	KH_2PO_4	0.2 gram
$MgSO_4 \cdot 7H_2O$	0.1 gram	Distilled H_2O	1000.0 ml.
$CaSO_4$	0.1 gram		

Total = 0.14% solution by weight

NO_3/NH_4 ionic ratio of 50/50

K_2HPO_4	0.2 gram	$MgSO_4 \cdot 7H_2O$	0.1 gram
KH_2PO_4	0.2 gram	$(NH_4)_2HPO_4$	0.3 gram
KNO_3	0.5 gram	$CaSO_4$	0.1 gram
		Distilled H_2O	1000.0 ml.

Total = 0.14% solution by weight

NO_3/NH_4 ionic ratio of 0/100

K_2HPO_4	0.2 gram	$(NH_4)_2HPO_4$	0.6 gram
KH_2PO_4	0.4 gram	$CaSO_4$	0.1 gram
$MgSO_4 \cdot 7H_2O$	0.1 gram	Distilled H_2O	1000.0 ml.

Total = 0.14% solution by weight

One liter of each of these solutions contained approximately 0.13 gram of nitrogen. For use seven volumes of water were added to three volumes of solution giving a concentration of 0.06 per cent by weight of nutrient salts in the diluted solution. Six-thousandths per cent by weight was nitrogen.

Tables 8 and 9 and figure 19 list data secured when solutions with different NO_3/NH_4 ionic ratios were used.

In all three solutions, plants supplied with nitrate nitrogen reached their greatest length and formed coenocysts more quickly than the others (fig. 27). Many such plants contained coenocysts after sixteen days.

Most plants on media with NO_3/NH_4 ionic ratio of 50/50 were in vegetative condition after twenty-four days (fig. 28). Plants with nitrate nitrogen were narrower in the rhizoidal portion than those with two nitrogen sources or with ammonium nitrogen only (figs. 27–29). Many of the plants that were supplied with ammonium nitrogen had bulb-like enlargements at the rhizoidal end (fig. 29). In all three solutions the longest sacs were produced on media with nitrate nitrogen (table 8, fig. 19). At the end of twenty-four days, the number of sacs in vegetative condition was much greater on

TABLE 8. *Effects on cell size of clone 8B2 of various culture media with different NO_3/NH_4 ionic ratios solidified with 1.5 per cent agar and grown at an average temperature of 17.5° C.*

Medium	NO_3/NH_4 ionic ratio	Mean length in mm. of 100 sacs after		
		8 days	16 days	24 days
Bristol's	100/0	0.14	0.47	0.70
	50/50	0.18	0.45	0.46
	0/100	0.13	0.26	0.26
Detmer's	100/0	0.32	0.50	0.90
	50/50	0.18	0.20	0.30
	0/100	0.13	0.19	0.30
Pringsheim's	100/0	0.16	0.54	0.76
	50/50	0.14	0.16	0.61
	0/100	0.17	0.21	0.28

media with low NO_3/NH_4 ionic ratios than it was on media with high ratios (figs. 27–30). Figure 19 shows that the results were similar for all three solutions.

TABLE 9. *Effects on the growth of clone 8B2 of various culture media with different NO_3/NH_4 ionic ratios used in liquid form at a temperature of 17.5° C.*

Medium	NO_3/NH_4 ionic ratio	pH		Color intensity	Amount centrifuged from one flask (ml.)	Observations
		At beginning of experiment	After 36 days			
Bristol's	100/0	6.7	6.6	2 –	0.03	Gametes numerous. Most cells spherical
	50/50	6.6	6.4	2	0.07	More sacs than are usual in a liquid culture (fig. 31).
	0/100	6.1	6.0	2 –	0.04	Gametes numerous. Cells mostly spherical.
Detmer's	100/0	6.5	6.3	1	0.03	More dead cells than living ones.
	50/50	4.0	3.9	1	0.03	Cells spherical. Most of them dead.
	0/100	4.3	4.0	1	0.03	Cells spherical. Most of them dead.
Pringsheim's	100/0	6.1	6.3	2 –	0.03	Many cells with lobes separated by septa. Dead cells present but not as numerous as in Detmer's solution.
	50/50	6.6	6.7	0	0.01	Heavy precipitate present, some gametes and many dead cells.
	0/100	6.6	6.7	1	0.04	Cells mostly spherical. Many zygotes and many dead cells.

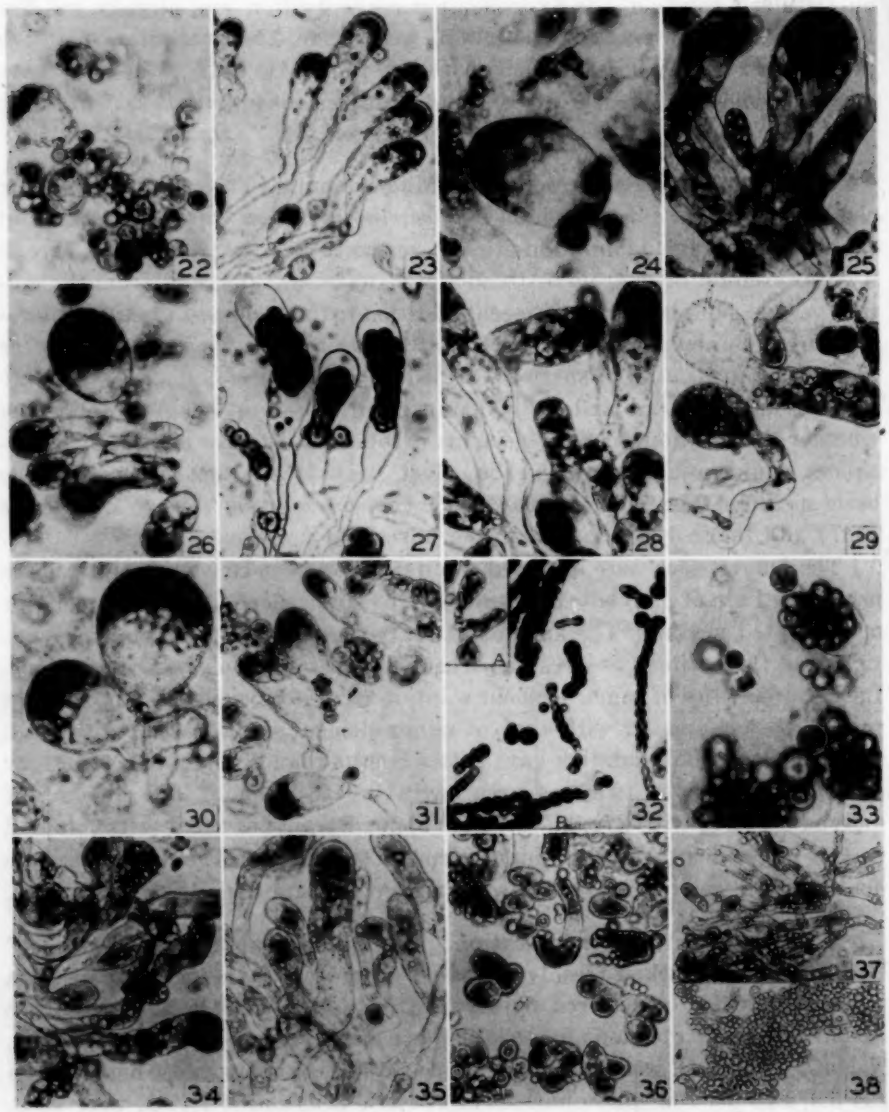
With Bristol's solution used in liquid form, growth was best when both nitrate and ammonium nitrogen were present. In two of the cultures based on Detmer's solution, the hydrogen-ion concentration was already too low for good growth when the inoculations were made. The precipitate that was present in Pringsheim's solutions with low NO_3/NH_4 ionic ratios may have removed some needed element from the solution. It is apparent that presence or absence of agar modifies the effect of varying NO_3/NH_4 ratios.

3. Effect of Minor Elements and Molybdenum. The quantity of minor elements required for growth of *Protosiphon* is almost certainly present in the form of unavoidable impurities in reagents even when rigorous care is used to exclude them from distilled water, nutrient salts, and from the culture vessels. Molybdenum is a recent addition to the supposed essential micro-elements. Steinberg (1936) showed that the decrease in yield of *Aspergillus niger* upon utilization of sucrose purified by alcohol was due almost entirely to the removal of zinc and molybdenum. Cultures were set up to determine whether the addition of micro-elements to solutions used for culture of *Protosiphon* would produce a measurable effect. Bristol's solution was used as the basic medium. The formulae for minor element solution (Craig & Trelease 1937) and for molybdic acid solution have been previously listed.

The longest sacs were obtained when 0.06 per cent Bristol's solution was used with 1 ml. of molybdic acid and 2 ml. of minor element solution per liter of undiluted medium. The amount of centrifugate obtained from this solution was three times as great as when Bristol's solution was used alone. Larger quantities of minor element solution were not beneficial, and the sacs produced were smaller with 4 ml. of minor element solution than with 2 ml. One ml. of molybdic solution gave better results than 2 ml. and the quantity of centrifugate was twice as great with the addition of this amount of molybdic acid as with Bristol's solution alone. Because of the results obtained in this experiment, 2 ml. of minor element solution and 1 ml. of molybdic acid solution were regularly added to a liter of undiluted Bristol's solution.

4. Hydrogen-Ion Concentration. The hydrogen-ion concentration of Bristol's solution when freshly prepared according to the original formula is pH 5.3. It can be lowered by substituting di-basic potassium phosphate for all or part of the mono-basic salt. For concentrations lower than pH 7.4, N NaOH or KOH was used. For hydrogen-ion concentrations higher than pH 5.3, 1.25 per cent phosphoric acid, N citric acid and N H_2SO_4 were used. Hydrogen-ion concentrations were adjusted in different ways in order to determine whether the effects produced were due to hydrogen or to other ions present.

It was found that growth was slower at first in cultures with alkaline reaction, but that these cultures remained green longer than those with acid


22
23
24
25
26
27
28
29
30
31
A
32
B
33
34
35
36
37
38

reaction. Microscopic examination showed that under the same conditions plants from alkaline cultures did not form coenocysts as soon as those from acid media (see also table 8). Evidence that growth continues longer in alkaline media was obtained when some flasks from a series with pH values ranging from pH 4.2 to pH 9.2 were centrifuged after 24 days growth and others from the same series were allowed to grow for 11 weeks. In flasks with an initial hydrogen-ion concentration of pH 4.2, the amount of centrifugate at the end of each period was 0.07 ml. At pH 5.1, the amount of centrifugate was 0.04 ml. at the end of 24 days and 0.08 ml. at the end of 11 weeks. At pH 8.4, the yield was 0.10 ml. after 24 days and 0.20 ml. after 11 weeks.

Another effect of alkaline media, especially noticeable in liquid cultures, is the inhibition of growth in the rhizoidal portion of the sacs. In figure 33, spherical cells from a liquid culture with pH 7.4 are filled with spherical aplanospores. In figures 31 and 36 thalli from liquid cultures with pH approximately 6.5 have developed rhizoidal portions.

Good growth was secured at pH 9.5 on both liquid and solid media. On the acid side, there was good growth on solid media at pH 3.4, but when this medium was used in liquid form, the liquid remained clear and the centrifugate contained only a few cells. This is further evidence of an increase in

Explanation of figures 22–38

FIGS. 22–32, 34–38 × 100. FIG. 33 × 300. FIG. 22. Spherical cells from clone 8*B*2 growing for 24 days in 0.06% Bristol's solution (liquid). FIG. 23. Sacs about 0.75 mm. long from a culture of clone 8*B*2 on 0.06% Bristol's solution with 0.75% agar 24 days after inoculation. FIG. 24. Thalli from clone 8*B*2 grown for 24 days on 0.06% Bristol's solution with 4.5% agar. FIG. 25. Sacs 0.25–0.37 mm. long from clone 8*B*2 grown for 24 days on 0.06% Pringsheim's solution with 2% agar. FIG. 26. Sacs from 0.1–0.2 mm. long from clone 8*B*2 grown for 24 days on 0.06% Pringsheim's solution with 3% agar. FIG. 27. Sacs about 0.5 mm. long and tapering to a point from clone 8*B*2 grown 25 days on 0.06% Bristol's solution with an ionic ratio of 100 NO_3/O NH_4. FIG. 28. Vegetative sacs from clone 8*B*2 grown 24 days on 0.06% Bristol's solution with an ionic ratio of 50 NO_3/50 NH_4. FIG. 29. Sacs from clone 8*B*2 grown 24 days on 0.06% Bristol's solution with an ionic ratio of 0 NO_3/100 NH_4. The sac in the upper center of the figure is 0.25 mm. long and 0.04 mm. wide in the green part. FIG. 30. Sacs from clone 8*B*2 grown for 24 days on 0.06% Pringsheim's solution with an ionic ratio of 0 NO_3/100 NH_4. FIG. 31. Sacs from clone 8*B*2 grown for 36 days in 0.06% Bristol's solution (liquid) with an ionic ratio of 50 NO_3/50 NH_4. The sacs are from 0.12 mm. wide to 0.15 mm. long and from 0.03 mm. to 0.05 mm. in diameter. FIG. 32. A, Sac from clone 8*B*1 after 12 days growth in 0.06% Bristol's solution without Ca and solidified with 1.5% agar. B, Sacs from the same culture after 18 days with coenocysts filling the entire sac. FIG. 33. Spherical cells filled with growing aplanospores from clone 6*B*1 after 18 days growth in 0.06% Bristol's solution (liquid) with pH 7.4. FIG. 34. Sacs 0.3 mm. long from clone 8*B*2 grown for 24 days on 0.06% Bristol's solution – Ca and solidified with 1.5% agar. FIG. 35. Sacs 0.37 mm. long from clone 8*B*2 grown for 24 days on 0.06% Bristol's solution with 0.006% sodium oxalate and 1.5% agar. FIG. 36. Cells from clone 2*B*1 centrifuged from 0.06% Bristol's solution (liquid) with 0.5% fructose after 24 days growth. FIG. 37. Sacs from clone 2*B*1 grown 12 days on 0.06% Bristol's solution with 0.5% raffinose and 1.5% agar. FIG. 38. Sacs from clone 2*B*1 grown for 12 days on 0.06% Bristol's solution with 0.5% mannose and 1.5% agar.

growth when agar is added to the medium. At pH 4.2, there was good growth in liquid and 0.04 ml. of centrifugate was obtained from a flask after 18 days.

In twenty cultures, some with media in which the initial reaction was acid and others with alkaline media, the final hydrogen-ion concentrations were represented by pH values between 6 and 7. The optimum concentration for *Protosiphon* is probably within this range although good growth was secured in a much wider range.

5. Effect of Sodium Oxalate on the Growth of Protosiphon. Hopkins and Wann (1926, 1927) pointed out that iron can be almost completely removed from alkaline solutions by adsorption on calcium phosphate precipitate and that the lack of iron can be a limiting factor for growth of *Chlorella*. Inasmuch as many of the alkaline solutions used to test the effect of hydrogen-ion concentration contained precipitates a question arose concerning the possible effects of those precipitates.

Omission of calcium compounds lessened the difficulty with precipitates and apparently did not interfere with growth of the algae as determined quantitatively. One effect noted was that in one of the calcium-free cultures, there were odd-shaped sacs (fig. 32A) that lacked a rhizoidal portion. After eighteen days, the sacs contained coenocysts that were distributed throughout their lumens, and there was no clear rhizoidal portion (fig. 32B).

It seemed desirable to reduce the calcium content of the culture medium to a very low minimum in order to determine whether such a solution would support the growth of *Protosiphon*. Pringsheim (1926b) used concentrations of 0.006, 0.0125, 0.05, and 0.1 per cent sodium oxalate to precipitate calcium from nutrient solutions used to culture algae. He reported that algae which do not require calcium were not inhibited in their development by the presence of these concentrations of sodium oxalate, but he adds that traces of calcium sufficient for growth may be assimilated in the presence of oxalate.

Concentrations of sodium oxalate similar to those used by Pringsheim were added to modified Bristol's solution with calcium omitted from the

TABLE 10. *Effect on the growth of clone 8B2 of 0.06 per cent Bristol's solution in 1.5 per cent agar without calcium and with the addition of sodium oxalate at 16.5° C.*

Medium	Mean length in mm. of 100 sacs after	
	12 days	24 days
0.06% B. (control)	0.45	0.45
0.06% B. – Ca (control)	0.35	0.44
0.06% B. + 0.006% $Na_2C_2O_4$	0.33	0.44
0.06% B. + 0.0125% $Na_2C_2O_4$	0.33	0.55
0.06% B. + 0.025% $Na_2C_2O_4$	0.19	0.26
0.06% B. + 0.05% $Na_2C_2O_4$	0.15	0.06
0.06% B. + 0.1% $Na_2C_2O_4$	0.16	0.06

formula in an attempt to precipitate as well all calcium present as impurities. Bristol's solutions with and without calcium were used as controls (table 10). All the solutions were perfectly clear both before and after sterilizing. It was observed that a visible precipitate was formed when 0.0005 per cent calcium chloride was added to a solution containing 0.0003 per cent sodium oxalate. The amount of calcium compounds present in the media must then have been less than 0.0005 per cent.

Sacs were smaller after 24 days than after 12 days on the cultures with 0.05 per cent and 0.1 per cent $Na_2C_2O_4$ because the sacs had continued to form gametes for a longer time than in some of the other cultures. In all the cultures, the plants were still in vegetative condition after twenty-four days (figs. 34, 35). On cultures with the higher concentrations of sodium oxalate, the smaller size of the cells appeared to be due to concentration rather than to a toxic effect of the salt.

In liquid cultures, the growth was good and the amount of centrifugate from flasks with 0.006 per cent sodium oxalate was greater than from any of the others not excepting the control cultures. The interpretation of these data is considered in the discussion.

B. Organic Media

1. Carbohydrates. In preliminary experiments it was observed that growth was stimulated by small quantities of glucose. Experiments were set up to determine the optimum concentration of glucose and to compare its effect with that of other carbohydrates on the growth of *Protosiphon*. Tables 11, 12 and figure 20 summarize data for effects on the growth of *Protosiphon* of concentrations of 0.25 and 0.5 per cent of a pentose and a hexose from the monosaccharide sugars, a disaccharide, and a polysaccharide, added to 0.06 per cent Bristol's solution.

Twenty-five-hundredths per cent dextrose produced more growth in liquid cultures and larger sacs on solid media than 0.5 per cent dextrose.

TABLE 11. *Effects of certain sugars added to 0.06 per cent Bristol's solution with 1.5 per cent agar on the growth of clone 2B1 at a temperature of 20.5° C.*

Carbohydrate	Average length in mm. of 100 sacs after			
	6 days	12 days	18 days	24 days
0.25% dextrose	0.03	0.23	0.47	0.54
0.5% dextrose	**0.04**	0.26	0.30	0.32
0.25% inulin	0.03	0.18	0.22	0.25
0.5% inulin	0.01	**0.47**	**0.47**	**0.75**
0.25% sucrose	**0.04**	0.18	0.30	0.30
0.5% sucrose	0.03	0.32	0.37	0.43
0.25% xylose	0.01	0.07	0.14	0.14
0.5% xylose	0.02	0.03	0.03	0.10

This observation as well as some made in other experiments indicates that the optimum concentration of dextrose may be less than 0.25 per cent. Five-tenths per cent inulin produced the largest sacs on solid media and the greatest amount of centrifugate in liquid media. When it is used in liquid media, the results are very noticeable and large well developed sacs are found instead of the spherical ones that usually predominate in liquid media. Although in the present experiment larger sacs were produced on solid media

TABLE 12. *Effects on the growth of clone 2B1 of certain sugars added to 0.06 per cent Bristol's solution (liquid form) at 20.5° C.*

Amount of sugar	pH		Color intensity	Volume centrifuged from one flask (ml.)	Observations
	At beginning of experiment	After 24 days			
0.25% dextrose	6.0	6.6	4	0.055	Small cells with one or two coenocysts.
0.5% dextrose	6.0	6.6	4 –	0.07	Small cells with one or two coenocysts.
0.25% inulin	6.2	7.0	4 –	0.09	Sacs 0.12 mm. long in vegetative condition. Many zygotes.
0.5% inulin	6.2	7.0	4	0.12	Sacs 0.35 mm. long in vegetative condition.
0.25% sucrose	6.3	6.4	2	0.05	Small cells with single coenocysts 0.02 mm. in diameter.
0.5% sucrose	6.3	6.4	2 –	0.03	Small cells with single coenocysts 0.02 mm. in diameter.
0.25% xylose	5.1	5.9	3	0.06	Sacs 0.12 mm. long most of them in vegetative condition.
0.5% xylose	5.2	5.8	1	0.01	More dead than living cells. Some healthy looking sacs 0.1 mm. long.

with 0.5 per cent sucrose than with 0.25 per cent sucrose, the results obtained from liquid cultures and from other experiments indicate that the lower concentration of sucrose is more effective in stimulating growth of *Protosiphon*.

An experiment with higher concentrations of the same sugars shown in tables 11 and 12 gave further indication that higher concentrations are less effective than lower ones. Sacs in 1 per cent inulin were a little longer than they were in 0.5 per cent inulin, but inasmuch as this carbohydrate dissolves with difficulty in cold water and there was a ring of precipitate at the surface of the liquid in the flasks, it was apparent that the amount of inulin in the solution was less than 1 per cent.

Because equal concentrations of the carbohydrates used in the foregoing experiment did not react in the same way, it seemed desirable to use others and compare their effects on the growth of *Protosiphon*. Table 13 and figure 21 present data for the results obtained with the addition of two types of monosaccharides, a disaccharide, and a trisaccharide to 0.06 per cent Bristol's solution used to culture *Protosiphon*.

TABLE 13. *Effect of the addition of certain sugars to 0.06 per cent Bristol's solution with 1.5 per cent agar on the length of sacs of clone 2B1 at a temperature of 20° C.*

Concentration of sugar	Mean length in mm. of 100 sacs after			
	6 days	12 days	18 days	24 days
0.25% fructose	0.01	0.13	**0.55**	0.55
0.5% fructose	0.03	0.08	0.12	**0.75**
0.25% maltose	**0.08**	0.22	0.25	0.25
0.5% maltose	0.05	0.18	0.21	0.31
0.25% mannose	0.01	0.03	0.18	0.20
0.5% mannose	0.01	0.05	0.31	0.55
0.25% raffinose	0.01	0.19	0.25	0.33
0.5% raffinose	0.03	**0.26**	0.26	0.29

In this group of sugars, fructose gave the most growth and the longest sacs at the end of 24 days. Sacs on medium with 0.5 per cent mannose were much longer than those on the same concentration of maltose and raffinose, although for the first twelve days growth on mannose was slower than on either raffinose or maltose (figs. 37, 38). In liquid cultures, the greatest amount of centrifugate was obtained from media with mannose and fructose. Many small sacs with lobes separated by septa were observed in the liquid cultures with 0.5 per cent fructose (fig. 36).

2. Proteins. Six flasks of beef extract (beef extract, 3 grams; sodium chloride, 5 grams; peptone, 10 grams; distilled water, 1000 ml.) diluted to a concentration of 0.06 per cent by weight were inoculated with clone 3*B*1. Growth was very good and appeared to be concentrated at the bottom of the flasks in contrast to the heavy surface rings when sugars were used.

Good growth was also secured in solution with no nutrient but peptone. A dilution of 0.04 per cent gave better results than either 0.02 or 0.08 per cent peptone dilutions. A solution containing peptone and 0.06 per cent Detmer's solution also produced good growth of *Protosiphon*.

BIOLOGICAL LABORATORY, FORDHAM UNIVERSITY
NEW YORK

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 1, PP. 38–56 JANUARY, 1947

STUDIES IN THE CARYOPHYLLACEAE—III. A SYNOPSIS OF THE NORTH AMERICAN SPECIES OF ARENARIA, SECT. EREMOGONE FENZL

BASSETT MAGUIRE

The following is an enumeration of the North American species of *Arenaria*, all perennial, bearing narrowly linear and pungent or setaceous leaves, flower-discs that are provided with more or less conspicuous glands at the base of, and externally affixed to the stamens, and firm-walled capsules dehiscing by 6 teeth. In most species of this group, the antisepalous gland is conspicuously enlarged, entire or bilobed, and the alternate glands inconspicuous or obsolete. Less often are the ten glands of equal development, or altogether obsolete.

There is little doubt that American species falling into the characterization given above are closely interrelated and must be interpreted as belonging to a single natural section, notwithstanding the contrary disposition by the eminent Caryophyllologist, F. N. Williams.[1] Critical examination of an abundance of American material fails to support the segregation of species with enlarged antisepalous glands into the subgenus *Pentadenaria*. Indeed this condition obtains in most of the American species assigned by Williams (and essentially so maintained by Pax and Hoffman[2]) to both the subgenera *Eremogone* and *Pentadenaria*, and the character must be considered, at least with our species, of questionable value as determinant for subgeneric or sectional segregation.

Relationships among members of the American *Capillaris*-group are complex and obscure. Within it little clear-cut specific differentiation has taken place, or at least most species are so variable within themselves as to transgress all specific lines, removing discontinuity, and to leave only emphatic nodes in a basally almost continuous series.

If we consider *A. capillaris*, in the major western hemisphere representation the boreal subsp. *americana*, as the primitive and deriving member of the group—a position logically to be taken because of the chiefly whole-arctic distribution of the genus, and morphological mergence of the subspecies with austral presumptive derivatives—three principal lines of differentiation have taken place, these well correlated with geographic divergence and relative isolation.

1. Most directly differentiation has been made into *A. aculeata* and the

[1] A Revision of the genus Arenaria Linn. Jour. Linn. Soc. **33**: 334. 1898.
[2] Caryophyllaceae in Engler & Prantl, Nat. Pflanzenf. **16C**: 316. 1934.

more poorly segregated *A. pumicola*, *A. aberrans*, and *A. ursina*, all held together by obtuse hyaline-margined sepals, open inflorescence, and general habit.

2. The subsp. *americana* merges into *A. Kingii* where their ranges are coincident; into the subsp. *Kingii* in northern Nevada and southeastern Oregon, and into the subsp. *uintahensis* in northern Utah. *A. macradenia* seems to be a southern outgrowth of *A. Kingii*—possibly through the var. *glabrescens*.

3. The *A. congesta–A. Fendleri* complex. Habitally these two species resemble the subsp. *americana*, but have differentiated from their precursor and between themselves in the achievement of a congested inflorescence on the one hand and acuminate-attenuate sepals on the other. *A. Eastwoodiae* is an obvious Colorado Plateau derivative of *A. Fendleri*. The far disjunct desert range *A. stenomeres*, on morphological grounds, chiefly acuminate-attenuate sepals, seems to be related to *A. Fendleri*.

The position of *A. Hookeri* and *A. Franklinii* is obscure. While they both have developed cephaloid inflorescences, in habit they more resemble *A. Nuttallii* Pax, of the section *Alsine*.

The accompanying chart suggests diagrammatically the possible relationships and lines of derivation of the several species in the *Capillaris*-group.

Study in the Caryophyllaceae has inevitably been attended by protests of weak characterization in the family. Certainly this condition obtains for the group here under consideration. "Critical" specific characters are feeble. The interpretation of populations, specific and subspecific, depends largely on the accurate evaluation of the interplay of sepal, leaf, and inflorescence form. Gland size and disposition, seed, and rootstock offer supporting characterization. Of no little aid is the final summation of intangibles that comes of familiarity with the plants, and that give populations an "appearance"

or "look"—indefinite properties that defy descriptive analysis. Considerable weight has been also given to segregation from correlatable natural ranges. The weight attached to and the importance of all of these criteria is evident from the body of the paper.

SECTION EREMOGONE FENZL IN ENDL. GEN. **1**: 967. 1840.

Sect. *Pentadenaria* Williams, Bull. Herb. Boiss. **3**: 598 (at least as to American species). 1895. Subg. *Pentadenaria* Williams, Jour. Linn. Soc. **33**: 334 (at least as to American species). 1898. Subg. *Euarenaria* sect. *Eremogoneae* Williams, Jour. Linn. Soc. **33**: 338 (at least as to American species). 1898.

Flower-disc with more or less prominent glands at the base and externally adnate to the 10 stamens, the antisepalar glands usually more prominent and the antipetalar glands inconspicuous or obsolete, or all glands inconspicuous, even sometimes essentially obsolete; sepals more or less indurate at the base; capsule more or less indurate, partially dehiscing along the commissural sutures, each valve-apex in turn bidentate; leaves narrowly linear and more or less pungent, setaceous or subulate; perennial, frequently suffrutescent.

KEY TO THE SPECIES

1. Sepals obtuse, or merely acutish or apiculate.
   2. Inflorescence open (at least at full maturity), more or less dichotomous.
      3. Leaves recurved or flexuous, mostly (except in alpine forms) more than 2 cm. long; stems frequently leafy; seed 2.0–2.5 mm. long. 1. *A. capillaris americana.*
      3. Leaves aculeate or ascending, pungent, or fleshy, essentially basal, mostly 2 cm. or less long; seed 2.5–3.0 mm. long.
         4. Leaves stiffly pungent; plants characteristically glaucous and matted. 2. *A. aculeata.*
         4. Leaves more or less fleshy or not stiffly pungent; plants usually neither glaucous nor matted.
            5. Leaves strictly ascending, sepals 3–4 mm. long, capsules 4.5–5.5 mm. long. 3. *A. pumicola.*
            5. Leaves aculeate or recurved.
               6. Leaves aculeate, 1–2 cm. long; sepals 4–5 mm. long, capsules 7–9 mm. long. 4. *A. aberrans.*
               6. Leaves more or less recurved, 0.5–1.0 (1.5) cm. long; sepals 3–4.5 mm. long, capsules 3–5 mm. long. 5. *A. ursina.*
   2. Inflorescence congested, subcongested, or umbellate. 6. *A. congesta.*
1. Sepals acute to acuminate.
   2. Inflorescence open (at least at full maturity), more or less dichotomous.
      3. Sepals narrowly acute to acuminate.
         4. Petals broadly oblong-elliptic to oblanceolate, entire, retuse or somewhat erose; glands obvious or conspicuous; plants of the Rocky Mountain and Colorado Plateau.
            5. Stems glandular-puberulent, with 5 or more pairs of leaves; glands oval-oblong, ca. 0.5 mm. long; plants of the southern Rocky Mountain and high Colorado Plateau. 7. *A. Fendleri.*
            5. Stems glabrous or glandular, leaves essentially basal; glands oblong-truncate, 1–2 mm. long; plants of desert regions, Colorado Plateau. 8. *A. Eastwoodiae.*

4. Petals linear, emarginate, glands minute or obsolete; plants of the Great Basin. 11. *A. stenomeres.*

3. Sepals broadly acute.

4. Stems mostly 2–4 dm. tall and woody at the base; sepals 4.5–6.0 (6.6) mm. long; petals entire, erose, or retuse; glands 1–2 mm. long; plants of the Mohave Desert and lower Great Basin. 9. *A. macradenia.*

4. Stems mostly 2 dm. or less tall and not woody at the base; sepals 3.6–4.5 (6.0) mm. long; petals entire, erose, retuse, or cleft nearly to base; glands ca. 0.5 mm. long; plants of the Great Basin. 10. *A. Kingii.*

2. Inflorescence congested, subcongested, or proliferated.

3. Sepals 3–5 (6) mm. long, acute. 6. *A. congesta.*

3. Sepals (5.5) 6–15 mm. long, acuminate.

4. Stems leafy, glabrous; sepals 8.5–15 mm. long (5–6 mm. long in var. *Thompsoni*); dry slopes and plains of eastern Oregon and Washington. 12. *A. Franklinii.*

4. Stems not leafy, scabrid-puberulent; sepals 5.5–8.0 mm. long; plains and barren slopes and ridges, mostly east of the continental divide; Elko County, Nevada. 13. *A. Hookeri.*

1. ARENARIA CAPILLARIS Poir. Encycl. Meth. 6: 380. 1804.

KEY TO THE SUBSPECIES

Sepals usually 5–6 mm. long; (in ours) totally glabrous. *A. capillaris* subsp. *capillaris.*
Sepals usually 4.0–4.5 mm. long, inflorescence glandular. *A. capillaris* subsp. *americana.*

ARENARIA CAPILLARIS Poir. subsp. **capillaris** Maguire, subsp. nov.

A. capillaris Poir. Encycl. Meth. 6: 380, as to type. 1804.

A. formosa Fisch. ex DC. Prodr. 1: 402. 1824.

A. nardifolia Ledeb. Fl. Altaic 2: 166. 1830.

A. capillaris Poir. Grex c., ε. *formosa* (Fisch.) F. N. Wms. Jour. Linn. Soc. 33: 415, exclusive of American plants. 1898.

A. capillaris Poir. Grex c., ζ. *nardifolia* (Ledeb.) F. N. Wms. Jour. Linn. Soc. 33: 415. 1898.

Occurring sparingly in Alaska, differing from subsp. *americana* in its larger flowers and total glabrousness. Highly polymorphous, this extensive population has frequently been the object of extensive redivision. The Alaskan specimens are probably to be referred to the var. *nardifolia* (Ledeb.) Regel.

Type locality: "Cette plante a été recueillie par M. Patrin dans la Sibérie."

Distribution: Asia from the Angara-Sagan District (fide Hultén) to Alaska. Reported from the Northwest Territory (*A. nardifolia*) by Porsild.

Representative specimens: Healy, Alaska, July 17, 1922, *Anderson 1624* [var. *nardifolia* (Ledeb.) Regel].

ARENARIA CAPILLARIS Poir. subsp. **americana** Maguire, subsp. nov.

A. capillaris of American authors, not *A. capillaris* Poir.

A. nardifolia of American authors, not *A. nardifolia* Ledeb.

A. formosa of American authors, not *A. formosa* Fisch.

A. capillaris Poir. subsp. *formosa* (Fisch.) Maguire, Madroño 6: 24. 1941. Not *A. formosa* Fisch.

Caulibus (3) 5–15 (25) cm. longis, foliis lineari-subulatis, acutis, serrulatissimis, glabratis vel glanduloso-puberulentibus, foliis caulinis 2-jugis aliquando frondosis; inflorescentibus non congestis, rare subcongestis; pedicellis (2) 5–10 (15) mm. longis; sepalis (3) 3.5–4.5 (4.8) mm. longis; petalis (5) 6–10 mm. longis, late vel anguste elliptico-oblanceolatis; glandis ad 0.4 mm. longis; capsulis ovatis, ad apices fere granulari-pubescentibus, seminibus 2.0–2.5 mm. longis, non marginatis.

The American race may be recognized by its consistently smaller flowers; in subsp. *americana* the usual and average calyx length being 4.2 mm. with extreme range of 3.0–4.8 mm.; whereas the Asiatic races, including *A. formosa* Fisch. and *A. nardifolia* Ledeb. have the usual and average calyx length of 5.4 mm., the extremes at 3.6–6.6 mm., very few specimens having the shorter measurements. To the south of its range the subsp. *americana* is poorly separated from *A. aculeata* and *A. Kingii*.

The lower montane (and southern) form tends to be somewhat taller and to have somewhat larger flowers with more acutish sepals than boreal or alpine plants.

Type locality: Hurricane Ridge, Olympic Mountains, Clallam County, Washington, *J. W. Thompson 14162* (N. Y. Bot. Gard.).

Distribution: Mountains and plains, British Columbia and Alberta south in the mountains to central Oregon, Idaho, Montana, and northwestern Nevada. Possibly in Alaska.

Representative specimens: Skagit River, B. C., July 22, 1905, *J. M. Macoun* (Geol. Surv. Cana. 79578); Banff, Alberta, July 7, 1899, *W. C. McCalla 2410*; Challis, Custer County, Idaho, June 15, 1944, *Hitchcock & Muhlick 8976*; Wiessner Peak, Kootenai County, Idaho, July 8, 1892, *Sandberg et al. 589*; Ole Creek, Glacier National Park, Montana, June 30, 1934, *Maguire & Piranian 15711*; Mt. Stuart, Missoula, Montana, July 3, 1921, *Kirkwood 1105*; Moffats Diamond A Ranch, Elko County, Nevada, May 29, 1939, *York* sine no.; Virden, Kittitas County, Washington, June 8, 1935, *Thompson 11580*; Mt. Paddo, Washington, August 11, 1909, *Suksdorf* sine no.; Mt. Hood, Oregon, August 27, 1905, *Lyon 161*.

2. ARENARIA ACULEATA S. Wats. Bot. King's Expl. **5**: 40. 1871. Not *A. aculeata* Desv. Jour. de Bot. **3**: 221. 1816 (nomen nudum).

A. salmonensis Henderson, Bull. Torrey Club **27**: 343. 1900.

Type locality: Fremont's Pass, East Humboldt (Ruby) Range, Elko County, 6500 feet, in fruit, August, 1868, *S. Watson 170* (Gray Herb.).

Distribution: Dry gravelly slopes, from 6000 to 10,000 feet elevation; Beaverhead County, Montana, Custer, Blaine and Valley Counties, Idaho, to Wallowa and Baker Counties, Oregon, south to Modoc and Plumas Counties, California, northern Nevada, and Box Elder County, Utah.

Representative specimens: Anthony Lake Region, Blue Mountains, Baker County, Oregon, July 23, 1936, *Thompson 13444*; Crane Mountain, Lake County, Oregon, July 12, 1936, *Thompson 13238*; Strawberry Mountains, Grant County, Oregon, July 15, 1921, *Peck 10261*; Warner Mountains, Modoc County, California, August 8, 1935, *Wheeler 3809*; Sawtooth Mountains, Blaine County, Idaho, August 8–11, 1939, *Hitchcock & Martin 5730*; Bonanza, Custer County, Idaho, July 25, 1916, *McBride & Payson 3443*; Santa Rosa Range, Humboldt County, Nevada, July 22, 1937, *Train 496*; Lamoille Canyon, Ruby Range, Elko County, Nevada, July 22, 1945, *Maguire & Holmgren 22057*; Dunn Canyon, Raft River Mountains, Box Elder County, Utah, July 31, 1943, *Maguire & Holmgren 22198*.

3. ARENARIA PUMICOLA Coville and Leiberg, Proc. Biol. Soc. Wash. **11**: 169. 1897.

KEY TO THE VARIETIES

Leaves fleshy; stems hardly ligneous at the base. 1. *A. pumicola* var. *pumicola*.
Leaves not fleshy; stems ligneous at the base. 2. *A. pumicola* var. *californica*.

ARENARIA PUMICOLA var. **pumicola** Maguire, var. nov.

A. pumicola Coville and Leiberg, Proc. Biol. Soc. Wash. 11: 169, as to type. 1897.

A. pumicola is an unsatisfactorily distinct species and may finally have to be interpreted as a part of *A. aculeata*, as a subspecific or even varietal ecologic population.

Type locality: Pulverized pumice-stone, rim Crater Lake, altitude 2180 m., Klamath County, Oregon, August 13, 1896, *Coville and Leiberg 349* (U. S. Nat. Herb.).

Distribution: Apparently restricted to loose pumice, Klamath County, Oregon. Plants intermediate to the next are known from Josephine County, Oregon.

Representative specimens: Crater Lake, Oregon: *Cusick 2977*; *Heller 13457*; *Maguire et al. 15095*. Abbott Butte, Jackson County, Oregon, July 2, 1936, *Thompson 13050*, is intermediate to the var. *californica*.

ARENARIA PUMICOLA var. **californica** Maguire, var. nov. Caudice ligneo, caulibus 15–30 cm. altis; foliis vix succulentis, foliis caulinibus, non basilaribus.

As circumscribed here, the var. *californica* is not a strong natural population, but is set up about three dispersed collections, more woody and vigorous, and less fleshy than the typical race.

Type locality: Lake Valley, Lake Tahoe Region, California, July 27, 1911, *LeRoy Abrams 4779* (N. Y. Bot. Gard.).

In addition to the type, the following two collections are known to me: Lover's Leap, Horsetail Falls trail, El Dorado County, California, August 12, 1936, *Belshaw 2628*; "California," 1875, *Lemmon* sine no.

4. ARENARIA ABERRANS M. E. Jones, Contr. West. Bot. **16**: 37. 1930.

A. Rusbyi Greene, in Heller, Cat. N. Am. Pl. ed. 1. 49. 1898 (nomen nudum).

This species is a good, clear segregate closely derived from *A. capillaris* and related to *A. aculeata* and *A. pumicola*, but is sharply set off by its fleshy basally disposed leaves, large flowers, and relatively immense capsules.

Type locality: Dry hills, oak assn., 7000 ft. elevation, Mt. Dellanbough, Mohave County, Arizona, *Cottam 4159*, (Pomona; isotype at Brigham Young University).

Distribution: Apparently restricted to oak and yellow pine areas from 5500–9000 ft., Colorado and Kiabab Plateaus, Gila, Coconino, and Mohave Counties, Arizona.

Representative specimens: Hollow Canyon, Arizona, May 17, 1883, *Rusby 532*; Grand Canyon, Arizona, June 26, 1898, *McDougal 169*; between Payson and East Verde Bridge, Arizona, May 19, 1935, *Nelson & Nelson 1999*; South Gate, Grand Canyon, Coconino County, Arizona, June 27, 1935, *Maguire 12236*.

5. ARENARIA URSINA Robins. Proc. Am. Acad. **29**: 294. 1894.

Arenaria capillaris var. *ursina* (Robins.) Robins. Syn. Fl. N. Am. 1: 240. 1897.

Not so clearly a distinct derivative as the above from its *A. capillaris*.

Type locality: Dry hills, San Bernardino Valley, San Bernardino Mountains, Bernardino County, California, August, 1882, *S. B. & W. F. Parish* sine no. (Gray Herb.).

Distribution: Dry hills and slopes 7000–10,000 ft., San Bernardino, Inyo, Fresno, and Riverside Counties, California; possibly the range more extended.

Representative collections: Bear Valley, San Bernardino County, California, June 25, 1894, *Parish 3124*; Grapevine Mountain, California, June 9, 1891, *Coville & Funston 1764*; Black Mountain, Fresno County, California, July, 1900, *Hall & Chandler 591*.

6. ARENARIA CONGESTA Nutt. ex Torr. & Gray, Fl. N. Am. **1**: 178. 1838.

Perhaps the most widely distributed and polymorphous species in the *Capillaris*-group, *A congesta* is here interpreted as, in addition to the more extensive typical population, having developed ten more or less distinctive and partially geographically restricted variants.

The chief characters about which variation takes place, and upon which segregation has been made, is the degree of congestion of the inflorescence, form of the sepal apex, and to some extent the form and disposition of the leaves. Only the varieties *charlestonensis* and *crassula* depart from the important general habit of the species in having short basally disposed leaves. The theme of variation otherwise plays upon a proliferation, or better, a relaxation of the inflorescence, and the sepals becoming acute or acuminate as against the more prevalent obtuse condition. Neither of these modifications appears to be linked, but may appear independently or coincidentally.

Effort was made to separate the Sierran plants with umbellate inflorescence as a subspecies, distinct from the northern and eastern members of the species. This attempt was given up, however, since the typical form occurs concomitantly with it, and its character tends to appear throughout the general range of the species.

The most tenuous entity recognized is the var. *subcongesta*, wherein complete intermediacy is accomplished between *A. congesta* and the almost equally polymorphous *A. Kingii*. Because of this, however, no advantage can be seen in attempting to link the two populations specifically. To do so would necessitate sweeping together many of the more fluid species, viz., *A. congesta*, *A. Kingii*, and *A. capillaris* and derivatives, even perhaps *A. Fendleri*.

KEY TO THE VARIETIES

1. Sepals obtuse.
   2. Inflorescence compactly congested.
      3. Leaves 3–6 (8) cm. long, filiform. *A. congesta* var. *congesta*.
      3. Leaves 2–3 cm. long, 1–2 mm. wide, crassulus and subsucculent. *A. congesta* var. *crassula*.
   2. Inflorescence proliferating or umbeliate.
      3. Inflorescence proliferating, forming more or less loose, irregular cymes; sepals 4–5 mm. long; central Idaho and adjacent Montana and Wyoming, probably also in Colorado and Utah. *A. congesta* var. *expansa*.
      3. Inflorescence umbellate, the bracts arising approximately at the summit of the peduncle; sepals 3–4 mm. long; Sierra Nevada. *A. congesta* var. *suffrutescens*.

1. Sepals acute.
  2. Inflorescence compactly congested, the flowers essentially sessile.
    3. Leaves filiform, 3–8 cm. long; plants of central Idaho and adjacent Montana and Wyoming. *A. congesta* var. *cephaloidea.*
    3. Leaves not filiform, 1–2 cm. long, less than 1 mm. broad; leaves and sepals pungent; Charleston Mountains, Nevada. *A. congesta* var. *charlestonensis.*
  2. Inflorescence proliferating, or the flowers obviously pedicelled.
    3. Stems 15–20 cm. or more high, leafy; leaves (2) 3–8 cm. long, filiform, usually strict; dry slopes east of Cascade Divide, Oregon and Washington. *A. congesta* var. *prolifera.*
    3. Stems usually 15 cm. or less high, not leafy; leaves 2 cm. or less long, broader, usually divergent or recurved.
      4. Inflorescence usually little congested; sepals 4.0–5.0 (5.5) mm. long, weakly or not at all 3-nerved; dry slopes east of the Sierra Nevada; Great Basin. *A. congesta* var. *subcongesta.*
      4. Inflorescence usually more or less closely congested; sepals (5.0) 5.5–6.5 mm. long.
        5. Stems 5–10 cm. high; leaves usually strongly recurved; sepals conspicuously 3-nerved; Snake Range, White Pine County, Nevada. *A. congesta* var. *wheelerensis.*
        5. Stems 10–15 cm. high; leaves usually strict; sepals feebly or not at all 3-nerved; plants of Lassen and Modoc Counties, California, and adjacent Nevada. *A. congesta* var. *simulans.*

ARENARIA CONGESTA var. **congesta** Maguire, var. nov.

A. congesta Nutt. ex T. & G. Fl. N. Am. 1: 178, as to the type and most of the population. 1838.

Type locality: "Shady hills in the Rocky Mountain range, about Bear River of the Lake of Timpanogos."

Distribution: The most widespread assemblage within the species; plains and mountain slopes and ridges to 11,500 ft.; Washington and Montana to central California, and southern Nevada, Utah, and Colorado.

ARENARIA CONGESTA var. **crassula** Maguire, var. nov. Caulibus 15–20 cm. altis; foliis 1.5–3.0 cm. longis, 1–2 mm. latis, crassulis, subsucculentibus, basilaribus, inflorescentibus dense congestis; sepalis 3.5–4.0 mm. longis, obtusis, crassulis, subsucculentibus.

Type locality: Alpine slopes of Ashland Peak, 7500 ft., Siskiyou Mountains, Jackson County, Oregon, July 28, 1935, *Thompson 12358* (N. Y. Bot. Gard.). Striking in character; its habit, with the exception of the dense spheroid head and broad subsucculent leaves, is that of *A. pumicola*, suggesting a possible hybrid origin between *A. congesta* var. *congesta* and *A. pumicola.*

Distribution: Upper montane slopes, Siskiyou Mountains, southwestern Oregon and adjacent California.

Representative specimens: Marble Mountains, Siskiyou County, California: July 9, 1939, *Hitchcock & Martin 5324*; June 1901, *Chandler 1674*; Devil's Garden, September 12, 1935, Modoc County, California, *Wheeler 3980* (flowers large).

ARENARIA CONGESTA var. **expansa** Maguire, var. nov. Caulibus 15–30 cm. altis; foliis basilaribus filiformibus, 3–6 cm. longis; inflorescentibus proliferatis; sepalis 3–4 mm. longis, obtusis.

In habit like the varieties *congesta* and *prolifera*, but differing from the former by its open inflorescence, and from the latter by its smaller and obtuse sepals.

Type locality: Rocky granitic slopes near Wildhorse Creek, 25 miles S.W. Chilly, Custer County, Idaho, 7300 ft., July 22, 1941, *A. Cronquist 3309* (N. Y. Bot. Gard.). Cotype: north exposure, small canyon 4 miles N.E. Dickey, Custer County, Idaho, 7800 ft., July 15, 1941, *A. Cronquist 3137* (Intermountain Herb.).

Distribution: Central Idaho and adjacent Beaverhead County, Montana, and Yellowstone Park, Wyoming, perhaps more widely spread.

Representative specimens: Yellowstone National Park, Wyoming, *Maguire & Maguire 1157*; Gibbonsville, Lemhi County, Idaho, *Hitchcock et al. 3695*.

ARENARIA CONGESTA var. SUFFRUTESCENS (Gray) Robins.

Brewerina suffrutescens Gray, Proc. Am. Acad. **8**: 620, as to type. 1873.
Arenaria congesta Nutt. ex T. & G. var. *suffrutescens* (Gray) Robins. Proc. Am. Acad. **29**: 295. 1894.
A. suffrutescens (Gray) Heller, Muhlenbergia **6**: 96. 1910.

Within the var. *suffrutescens* two interesting forms occur: from Placer County south the population has glandular stems and more strict leaves, while to the northward from Plumas County to Josephine County, Oregon, the plants consistently have glabrous stems and longer leaves tending to become flexuous. If the population with umbellate inflorescence could be treated as a subspecies, these forms of obvious taxonomic significance would fall as varieties.

Type locality: Sierra Nevada above Cisco (and between Truckee and Donner Lake), Placer County, California, *Bolander & Kellogg* (Gray Herb.).

Distribution: Mountain slopes 5300 to 11,000 ft., Siskiyou Mountains and the Sierra Nevada Range, from Josephine County, Oregon, south to Tulare County, California.

Representative specimens: Pubescent form: Emigrant Gap (Placer County), California, May 28, 1882, *Jones 3278*; Emigrant Gap, June 19, 1917, *Heller 12741*; Hockett's Meadow, Tulare County, California, July 22, 1904, *Baker 4476*. Glabrous form: Genesee Valley, Plumas County, California, July 16, 1907, *Heller & Kennedy 8869*; Mt. Eddy, Siskiyou County, California, August 18, 1903, *Baker 3908*; Lake Mountain, Siskiyou Mountains, Josephine County, Oregon, July 7, 1939, *Hitchcock & Martin 5140*.

ARENARIA CONGESTA var. **cephaloidea** (Rydb.) Maguire, comb. nov.

A. cephaloidea Rydb. Bull. Torrey Club **39**: 316. 1912.

Similar in habit to var. *congesta*, but with lanceolate, acute, and somewhat pungent sepals.

Type locality: Open gravelly wood, Spokane County, Washington, August 10, 1902, *Kreager 617* (N. Y. Bot. Gard.).

Distribution: Essentially confined to central and northwestern Washington and adjacent Idaho, this variant has not been frequently collected. Reported from the Uinta Mountains, Utah, by Goodman (Ann. Mo. Bot. Gard. **18**: 284. 1931).

Representative specimens: Little Potlatch River, Latah County, Idaho, June 2, 1892, *Sandberg et al. 478*, cotype; dry prairies, Spokane County, Washington, June 27, 1884, *Suksdorf* sine no., cotype; St. Mary's River, northern Idaho, July 4, 1895, *Leiberg 1164*; Boise, Boise County, Idaho, June 2, 1944, *Hitchcock & Muhlick 8640*.

ARENARIA CONGESTA var. CHARLESTONENSIS Maguire, Bull. Torrey Club 72: 326. 1946.

Type locality: Harris Spring Summit Road, 18 miles south Kyle Canyon, 8500 ft., Charleston Mountains, Clark County, Nevada, August 2, 1938, *Train 2256* (N. Y. Bot. Gard.).

Known with confidence only by the type collection but strikingly marked by its short pungent basal leaves and pungent sepals. A collection from the nearby Sheep Range, *Alexander & Kellogg 1792*, is referred here with considerable uncertainty. The specimens have the habit and leaf characters of *A. Kingii* subsp. *compacta*, but the congested inflorescence more probably aligns them with *A. congesta*.

ARENARIA CONGESTA var. **prolifera** Maguire, var. nov.

A. Burkei Howell, Fl. N. W. Am. 1: 85. 1897. Based on the original description and the name *A. Fendleri* var. *subcongesta* S. Wats., but applied to plants of Oregon and Washington, and not to type of var. *subcongesta*.

A. congesta var. *subcongesta* (S. Wats.), Wats. Bot. Calif. 1: 69, as to specimens, but not as to type. 1876.

A. glabrescens Piper, Contr. U. S. Nat. Herb. 11: 261. 1906. Not *A. Fendleri* var. *glabrescens* S. Wats.

Var. *congesta* similis, sed inflorescentibus proliferatis et sepalis acutis.

Similar in habit to var. *congesta* and var. *expansa*, but differing in the open inflorescence from the former and in the longer acute sepals from the latter.

Type locality: Junction Crab and Wilson Creeks, 1600 ft., Douglas County, Washington, June 24, 1893, *Sandberg & Leiberg 294* (N. Y. Bot. Gard.). Cotype: high sagebrush slopes between Coulee City and Hartline, Grant County, Washington, June 16, 1935, *Thompson 11664* (N. Y. Bot. Gard.).

Distribution: Sagebrush plains and slopes eastern Washington, Oregon, and Alberta.

Representative specimens: Lake Chelan, Chelan County, Washington, June 12, 1936, *Kelly 1*; Almira, Lincoln County, Washington, June 22, 1933, *Thompson 9149*.

ARENARIA CONGESTA var. SUBCONGESTA (S. Wats.) S. Wats. Bot. Calif. 1: 69. 1876.

A. Fendleri var. *subcongesta* S. Wats. Bot. King's Expl. 5: 40, as to type. 1871.

A. Fendleri var. *glabrescens* S. Wats. Bot. King's Expl. 5: 40, as to cited specimens of Nevada. 1871.

A. Burkei Howell, Fl. N. W. Am. 1: 85, as to name, not specimens. 1897.

A weak variant representing transitional forms between *A. congesta* and *A. Kingii* var. *glabrescens*, and/or, perhaps *A. capillaris* subsp. *americana*. It is not impossible that the type of var. *subcongesta* may actually represent a depauperate specimen of the latter. I am unable to make pronouncement in this regard after careful examination of the type at Gray Herbarium, and an isotype at the New York Botanical Garden. Since the types have been associated historically with *A. congesta*, there is no justification for modifying the nomenclature or the association.

Type locality: East Humboldt (Ruby) Mountains, Elko County, Nevada, 8000 ft., July, 1868, *S. Watson 168* (Gray Herb.).

Distribution: Plants of inhospitable habitats, Great Basin from northern Nevada and adjacent California to Millard County, Utah, and Nye County, Nevada.

Representative specimens: "California" 1875, *Lemmon 40*; Arum, Nevada, May 9, 1893, *Jones* sine no.; Ruby Hill, Nevada, July 7, 1891, *Jones* sine no.; Cisco [Millard County], Utah, May 2, 1890, *Jones* sine no.; Sherman Peak, White Pine County, Nevada, August 4, 1939, *Hitchcock & Martin 5635*; Midas, Elko County, Nevada, June 10, 1940, *Holmgren 642*; Spruce Mountain, Elko County, Nevada, July 22, 1941, *Holmgren 1506*. The last three specimens are intermediate to var. *wheelerensis*.

ARENARIA CONGESTA var. **wheelerensis** Maguire, var. nov. Caulibus 5–10 (12) cm. altis; foliis innovationibus 1.2–1.5 (2.0) cm. longis; foliis cauliniis frequenter brevioribus; sepalis (5) 5.5–6.5 mm. longis, acutis 3-nerviis; petalis 6–10 mm. longis; inflorescentibus non dense aggregatis.

Type locality: Common, open bank in spruce-aspen belt about Lake Stella, 10,500 ft., Lehman Creek Basin, Mt. Wheeler, Snake Range, White Pine County, Nevada, August 4, 1941, *Maguire 21129* (N. Y. Bot. Gard.).

Distribution: Certainly a derivative of *A. congesta* and apparently localized in the high mountain region of northeastern Nevada and possibly adjacent Utah.

Representative specimens: Snake Range, White Pine County, Nevada, *Maguire 21155, 21095, Hitchcock & Martin 5635*; Elko County, Nevada, Holmgren *642, 1506*.

ARENARIA CONGESTA var. **simulans** Maguire, var. nov. Ab var. *wheelerensi* caulibus 10–15 cm. altis, foliis recurvatis; sepalis 1 (3)-nerviis differt.

Weakly separated morphologically from var. *wheelerensis*, but recognizable in its taller stems, usually recurved leaves, usually 1-nerved sepals, and discrete distribution.

Type locality: Plentiful in gravelly clay soil on an open slope east of Fredonyer Pass, elevation 5400 ft. Arid Transition Life Zone, Lassen County, California, June 23, 1938, *Heller 15198* (N. Y. Bot. Gard.).

Distribution: The mountain region of Modoc and Lassen Counties, California; and the Santa Rosa Range, Humboldt County, Nevada.

Representative specimens: Alturas, Modoc County, May 28, 1940, *Hitchcock 6728*; "Pot-Hole Springs" 30 mi. west Goose Lake, Modoc County, 1894, *Austin* sine no.; Madaline plains, June 1898, *Austin & Bruce* sine no.; Indian Summit, Santa Rosa Range, Humboldt County, Nevada, *Maguire & Holmgren 22504, 22514*.

7. ARENARIA FENDLERI A. Gray, Mem. Am. Acad. II. **4**: 13. 1849.

KEY TO THE VARIETIES

1. Sepals acuminate, 6–7.5 mm. long, inflorescence moderately glandular.
   2. Leaves 1–6 cm. long, ascending or recurved, inflorescence ascending.
      3. Leaves 3–6 cm. long. *A. Fendleri* var. *Fendleri*.
      3. Leaves 1–2 (3) cm. long. *A. Fendleri* var. *Porteri*.
   2. Leaves 6–10 cm. long, flexuous; inflorescence lax. *A. Fendleri* var. *diffusa*.
1. Sepals acute, 4–6 (7) mm. long, inflorescence densely glandular.
   2. Leaves 2–4 (6) cm. long; sepals 5–6 (7) mm. long. *A. Fendleri* var. *brevifolia*.
   2. Leaves 1–2 cm. long; sepals 4–5 (6) mm. long. *A. Fendleri* var. *Tweedyi*.

ARENARIA FENDLERI var. **Fendleri** Maguire, var. nov.

A. Fendleri A. Gray, Mem. Am. Acad. II. **4**: 13, as to type. 1849.
A. Fendleri A. Gray subsp. *genuina* Maguire, Madroño **6**: 23. 1941.

Type locality: Las Vegas, San Miguel County, New Mexico, *Fendler 57* (Gray Herb.).

Distribution: The major and most extensive population; plains and mountain slopes to the alpine belt; Albany and Carbon Counties, Wyoming (and possibly adjacent Nebraska), Colorado, in the mountains south in Arizona to the Huachuca Mountains, Cochise County, in New Mexico to the Oregon Mountains, Donna Ana County, and in Texas to Jeff Davis County; probably to be found in the states of Sonora and Chihuahua, Mexico.

ARENARIA FENDLERI var. PORTERI Rydb. Bull. Torrey Club **31**: 407. 1904.

Type locality: Grays Peak, altitude 13,000 ft., August 29, 1878, *M. E. Jones 716* (N. Y. Bot. Gard.).

Distribution: The alpine form confined to mountain peaks above timberline in Colorado, and the San Francisco Mountains, Coconino County, Arizona.

Representative specimens: Colorado: Mount Ouray, Ouray (?) County, August 20, 1901, *Baker 848, 849*; Berthoud Pass, Grand County, July 1903, *Tweedy 5533*; Silver Plume, Clear Creek County, *Shear 4600*; San Francisco Mountains, Coconino County, Arizona, August 28, 1938, *Little 4720*.

ARENARIA FENDLERI var. DIFFUSA Porter, Fl. Colo. Geol. Surv. Misc. Pub. **4**: 13. 1874.

A. laxiflora Rydb. Bull. Torrey Club **39**: 316. 1912.

Type locality: Ute Pass, Colorado, *Porter*.

Distribution: Favorable sites, grassy slopes and open woodlands to 10,000 ft. Colorado and northwestern New Mexico; perhaps throughout the range of the species.

Representative specimens: Bindermeer, Jefferson County, Colorado, July 4, 1921, *Clokey 4103*; Trinidad, Las Animas County, Colorado, July 3, 1937, *Rollins 1801*; El Porvenir, San Miguel County, New Mexico, October 23, 1939, *Drouet & Richards 3324*.

ARENARIA FENDLERI var. **brevifolia** (Maguire) Maguire, comb. nov.

A. Fendleri Gray subsp. *brevifolia* Maguire, Madroño **6**: 23, exclusive of var. *brevicaulis*. 1941.

Type locality: Burro Pass, La Sal Mountains, 11,300 ft., Grand County, Utah, *Maguire 17972* (Intermountain Herb.).

Distribution: Open slopes and meadows and open pine woodland, sometimes occupying drier areas, Grand and San Juan Counties, Utah; Montrose, Montezuma, and La Plata Counties, Colorado; Mohave and Coconino Counties, Arizona.

Representative specimens: Horse Gulch, La Sal Mountains, Grand County, Utah, July 15, 1911, *Rydberg & Garrett 8955*; Abajo Mountains, San Juan County, Utah, July 1–2, 1930, *Goodman & Hitchcock 1408*; Kiabab Forest, Coconino County, Arizona, June 28, 1935, *Maguire 12254*.

ARENARIA FENDLERI var. **Tweedyi** (Rydb.) Maguire, comb. nov.

A. Tweedyi Rydb. Bull. Torrey Club 31: 406. 1904.
A. Fendleri brevifolia, var. *brevicaulis* Maguire, Madroño 6: 23. 1941.

Type locality: La Plata Mountains, Colorado, July 15, 1896, *Tweedy* sine no. (N. Y. Bot. Gard.).

Distribution: Alpine peaks above timberline, La Plata Mountains, La Plata County, Colorado, and the La Sal Mountains, Grand and San Juan Counties, Utah.

Representative specimens: Mt. Peal, La Sal Mountains, San Juan County, Utah, July 17, 1911, *Rydberg & Garrett 8983*; Mt. Waas, La Sal Mountains, Grand County, Utah, July 13, 1933, *Maguire et al. 17982*.

8. ARENARIA EASTWOODIAE Rydb. Bull. Torrey Club **31**: 406. 1904.

KEY TO THE VARIETIES

Stems and inflorescence glabrous. *A. Eastwoodiae* var. *Eastwoodiae*.
Stems and inflorescence glandular. *A. Eastwoodiae* var. *adenophora*.

ARENARIA EASTWOODIAE var. **Eastwoodiae** Maguire, var. nov.

A. Eastwoodiae, Bull. Torrey Club 31: 406, as to type. 1904.

Type locality: Grand Junction, 1892, *Alice Eastwood* sine no. (N. Y. Bot. Gard.).

Distribution: Dry stony or sandy hills, mesas, and deserts, Daggett and Uintah Counties, Utah, Mesa County, Colorado, south to northern Coconino, Navajo, and Apache Counties, Arizona, and San Juan County, New Mexico.

Representative specimens: Delta, Delta County, Colorado, July 15, 1935, *Maguire 12458*; San Raphael Swell, Emery County, Utah, June 6, 1940, *Maguire 18451*; Inscription House, Coconino County, Arizona, June 11, 1938, *Peebles & Smith 13912*; Williams, Coconino County, Arizona, June 26, 1935, *Maguire 12234*.

ARENARIA EASTWOODIAE var. ADENOPHORA Kearney and Peebles, Jour. Wash. Acad. **29**: 475. 1939.

Type locality: Tuba, Coconino County, Arizona, *Peebles & Fulton 11856* (U. S. Nat. Herb. 1634508).

Distribution: Distribution that of var. *Eastwoodiae*, but tends to be more abundant on less favorable habitats, and the only form in extreme desert areas.

Representative specimens: De Beque, Mesa County, Colorado, May 26, 1910, *Osterhout 4247*; Aztec, New Mexico, May 1899, *Baker* sine no.; Natural Bridges, San Juan County, Utah, August 4–6, 1911, *Rydberg & Garrett 9414*; Fruita, Wayne County, Utah, June 30, 1940, *Maguire 19269*.

9. ARENARIA MACRADENIA S. Wats. Proc. Am. Acad. **17**: 367. 1882.

KEY TO THE SUBSPECIES AND VARIETIES

1. Sepals 5.5–6.5 mm. long; stems woody at the base; plants of the Mohave Desert. *A. macradenia* subsp. *macradenia*.
2. Petals conspicuously exceeding the sepals; cauline leaves 5 or more pairs; innovations seldom produced.

3. Cauline leaves mostly 5–8 pairs, ascending, 0.8–1.2 mm. broad. *A. macradenia* var. *macradenia*.
3. Cauline leaves mostly 6–12 pairs, strongly arcuate, 1.2–2.0 mm. broad.
4. Inflorescence and sepals glabrous. *A. macradenia* var. *arcuifolia*.
4. Inflorescence and sepals densely glandular. *A. macradenia* var. *Kuschei*.

2. Petals equaling or barely exceeding the petals; cauline leaves fewer than 5 pairs; innovations frequently produced. *A. macradenia* var. *Parishiorum*.

1. Sepals 4.0–5.5 mm. long; stems little or not at all woody at the base; plants of the Great Basin. *A. macradenia* subsp. *Ferrisiae*.

ARENARIA MACRADENIA subsp. MACRADENIA Maguire, Bull. Torrey Club **72**: 326. 1946.

A. macradenia S. Wats. Proc. Am. Acad. **17**: 367, as to type. 1882.

ARENARIA MACRADENIA subsp. MACRADENIA var. MACRADENIA Maguire, Bull. Torrey Club **72**: 326. 1946.

A. macradenia S. Wats. Proc. Am. Acad. **17**: 367, as to type. 1882.
A. congesta var. *macradenia* (S. Wats.) M. E. Jones, Proc. Cal. Acad. II. **5**: 626. 1895.
A. Fendleri var. *glabrescens* S. Wats. Bot. King's Expl. **5**: 40, in part. 1871.

Type locality: Near Mohave River, 1876, *Palmer 41* (Gray Herb.).

Distribution: Deserts, dry slopes and foothills to 5000 ft., Inyo and Los Angeles Counties, California; South Bern Mountains, Lower California; Mohave Desert to Clark County, Nevada; Washington County, Utah, and northern Mohave and Coconino Counties, Arizona.

Representative specimens: St. George, Washington County, Utah, 1877, *Palmer 53*; Caliente, Lincoln County, Nevada, September 7, 1938, *Train 2472*; Big Pine Creek, Inyo County, California, July 13, 1941, *Alexander & Kellogg 2545*; San Bernardino Mountains, Bernardino County, California, May 1882, *S. B. & W. F. Parish 1329*.

ARENARIA MACRADENIA subsp. MACRADENIA var. **arcuifolia** Maguire, var. nov. Sepalis 5.5–6.5 mm. longis, ciliolatis; foliis caulinibus fere 6–12 jugis, 1.2–2.0 mm. latis, valde arcuatis.

Type locality: Dry slopes, Mint Canyon, north of San Gabriel Mountains, May 25, 1923, *P. A. Munz 6792* (N. Y. Bot. Gard.).

Distribution: Dry slopes and foothills, San Gabriel, Liebre, and San Antonio Mountains, Los Angeles County, California. A strongly marked variant, recognized by the numerous, broad, arcuate cauline leaves and ciliate sepals.

Representative specimens: California: Liebre Mountains, Los Angeles County, June 20–23, 1908, *Abrams & McGregor 357*; Mohave Desert, May 25, 1882, *Pringle* sine no.; Kernville, Kern County, *Bacigalupi & Ferris 2476*.

ARENARIA MACRADENIA subsp. MACRADENIA var. **Kuschei** (Eastwood) Maguire, comb. nov.

A. Kuschei Eastw. Proc. Calif. Acad. IV. **20**: 140. 1931.

Differing from var. *arcuifolia* only in the prominent glandular pubescence of the inflorescence and sepals.

Apparently known only from the type: Forest Camp, Mohave Desert, California, July 12, 1929, *August Kusche* sine no. Herbarium California Academy of Sciences, No. 169243.

ARENARIA MACRADENIA subsp. MACRADENIA var. PARISHIORUM Robins. Proc. Am. Acad. **29**: 296. 1894.

A. congesta var. *Parishiorum* (Robins.) Robins. in Syn. Fl. N. Am. 1: 242. 1897.

This variant passes freely into var. *macradenia*.

Type locality: Common on mountains bordering on to the Mohave Desert [California], *S. B. & W. F. Parish 1330* (Gray Herb.).

Distribution: Desert ranges of southern California and southern Nevada to the Virgin Mountains, Mohave County, Arizona; "Lower California."

Representative specimens: White Mountains, Inyo County, California, May 13, 1930, *Duran 2637*; Clark County, Nevada: Valley of Fire, April 5, 1934, *Maguire et al. 4794*, and Charleston Mountains, June 6, 1936, *Clokey 7082*; Grand Wash, Mohave County, Arizona, April 26, 1941, *Maguire & Holmgren 20665*.

ARENARIA MACRADENIA subsp. FERRISIAE Abrams, Ill. Fl. Pacif. States **2**: 151. 1944.

Characterized by small flowers, less conspicuously nerved sepals, and somewhat less suffruticose base, this population is set off ecologically and to a large extent geographically from the major large-flowered desert race.

Type locality: Trail to Big Pine Lake along north fork of Big Pine Creek, elevation 9000–9500 ft., Inyo County (California), *Roxana S. Ferris 9000* (No. 230580 Dudley Herb.).

Distribution: Foothills and mountain slopes 5000–9500 ft., Inyo and Kern (according to Abrams) Counties, California, Lincoln County, Nevada, and Iron, Beaver Counties north to Utah County, Utah.

Representative specimens: Lone Pine [Inyo County], California, May 14, 1897, *Jones* sine no.; Granite Mountain Pass 15 mi. E. Milford, Beaver County, Utah, June 22, 1941, *Maguire 20998*; Mt. Nebo, Juab County, Utah, August 15, 1905, *Rydberg & Carlton 7579*.

10. ARENARIA KINGII (S. Wats.) M. E. Jones, Proc. Calif. Acad. Sci. II. **5**: 627. 1896.

This species is perhaps too broadly drawn, as was *A. congesta*. Yet if it is to be interpreted as more than a single polymorphic species, an overly great number of intermediate plants would be left without any place for assignment, or they would necessitate the erection of new specific names. But these would then rest on weak characters of indefiniteness and represent minor and loose assemblages without natural ranges. The name-bringing entity, the var. *Kingii*, might easily be lifted from the major part of the population. It is always recognizable (in flower) because of its bifid petals, but otherwise it is hardly to be distinguished from the var. *glabrescens*.

KEY TO THE SUBSPECIES AND VARIETIES

1. Sepals 3.6–4.5 (5.0) mm. long; capsule 4.5–6.3 mm. long; seed 1.5–2.0 mm. long.
   2. Petals white; inflorescence open, few- to many-flowered.
      3. Stems more or less leafy; leaves acerose, slender, mostly strict or ascending, 1–2 cm. long (ssp. *Kingii*).
         4. Petals bifid, inflorescence conspicuously glandular. *A. Kingii* var. *Kingii*.
         4. Petals entire or merely retuse, inflorescence inconspicuously glandular. *A. Kingii* var. *glabrescens*.
      3. Stems more or less scapose; leaves basally disposed, 0.5–1.5 cm. long, broadly subulate or trigonous, ascending or divergent.

4. Leaves trigonous, ascending, feebly ciliate; inflorescence including the sepals densely glandular; plants of the high central plateaus, Utah. *A. Kingii* subsp. *plateauensis.*

4. Leaves broadly subulate, tending to become widely divergent, prominently ciliate; inflorescence feebly glandular, sepals mostly glabrous; plants of the White Mountain and Mt. Whitney region, California. *A. Kingii* subsp. *compacta.*

2. Petals pink, inflorescence strict, few-flowered, caudex mostly few-branched; plants of the Charleston Mountains. *A. Kingii* subsp. *rosea.*

1. Sepals (4.5) 5.0–6.0 mm. long; capsule 5.5–7.2 mm. long; seed 2.0–2.5 mm. long; petals entire or occasionally bifid; plants of Wasatch Range, Utah, extending northward into Wyoming and Idaho. *A. Kingii* subsp. *uintahensis.*

ARENARIA KINGII subsp. **Kingii** Maguire, subsp. nov.

Stellaria Kingii S. Wats. Bot. King's Expl. 5: 39, as to type. 1871.

ARENARIA KINGII subsp. KINGII var. **Kingii** Maguire, var. nov.

Stellaria Kingii S. Wats. Bot. King's Expl. 5: 39, as to type. 1871.

Type locality: East Humboldt [Ruby] Mountains, 9000 ft. altitude, July, 1868, *S. Watson 164* (Gray Herb.).

Distribution: Dry slopes of the Great Basin ranges, particularly in eastern Nevada and west central Utah.

Representative specimens: Deep Creek Range, Juab County, Utah, July 1943, *Maguire & Holmgren 21934, 21939*; Desert Range Experiment Station, Millard County, Utah, June 18, 1941, *Maguire 20860*; Nevada: Pioche, Lincoln County, May 2, 1939, *Train 2684*; Pequop Range, Elko County, June 2, 1934, *Maguire et al. 5839*; Snake Range, White Pine County, June 18, 1941, *Maguire 20838*; Quinn Canyon Range, Nye County, June 6, 1945, *Maguire & Holmgren 25309.*

ARENARIA KINGII subsp. KINGII var. **glabrescens** (S. Wats.) Maguire, comb. nov.

A. Fendleri var. *glabrescens* S. Wats. in Bot. King's Expl. 5: 40, as to type. 1871.

Type locality: Toiyabe Mountains, 6000 ft. [Nye County] Nevada, July, 1865, *S. Watson 167* (type, Gray Herb.; isotype, N. Y. Bot. Gard.).

Distribution: Dry hills and slopes to 8000 ft., southeastern Oregon, southwestern Idaho, south to Esmeralda County, Nevada, and Inyo County, California, and in the basin ranges to Beaver and Iron Counties, Utah.

Representative specimens: Castle Peak, Nevada County, California, July 31, 1903, *Heller 7063*; Nevada: Boundary Peak, White Mountains, Esmeralda County, June 5, 1940, *Train 3951*; Paradise Range, Nye County, *Maguire & Holmgren 25397*; Izzenhood Ranch, Lander County, *Holmgren 542, 1100*; Golliher Pasture, San Jacinto, Elko County, *Maguire 16811, 16812, Holmgren 1372* (the three Golliher Pasture collections are intermediate to *A. capillaris americana*).

ARENARIA KINGII subsp. **compacta** (Coville) Maguire, comb. nov.

A. compacta Coville, Proc. Biol. Soc. Wash. 7: 67. 1892.

The culminative reductive alpine ecotype of *A. Kingii*. The type from Whitney Meadows is an exceedingly reduced specimen. Field study on the White Mountains where the subspecies grows abundantly shows all intergradation between the type and plants that are hardly separable from the subsp. *Kingii* var. *glabrescens.*

Type locality: Timberline, divide n.w. Whitney Meadows, Sierra Nevada, Tulare County, California, August 20, 1891, *F. V. Coville 1653* (U. S. Nat. Herb.).

Distribution: Alpine meadows and ridges, Mt. Whitney Region, Tulare County, and White Mountains, Inyo and Mono Counties, California.

Representative specimens: California: Piute Pass, Great Western Divide, July 22, 1934, Inyo County, *Ferris 8885*; Wyman Creek, White Mountains, August 1, 1945, *Maguire & Holmgren 26042*; Cottonwood Creek, White Mountains, Mono County, August 8, 1945, *Maguire & Holmgren 26153*; Johnny's Corral, White Mountains, Mono County, August 6, 1945, *Maguire & Holmgren 26106* (pink-flowered form).

ARENARIA KINGII subsp. **uintahensis** (A. Nels.) Maguire, comb. nov.

A. uintahensis A. Nels. Bull. Torrey Club **26**: 7. 1899.
A. aculeata var. *utahensis* (Nels.) Peck, Madroño **6**: 133, at least as to name. 1941.

Plants with bifid petals, but otherwise identical with the larger population, occur sporadically with it, mostly in the southern part of the range. Obviously, this form with bifid petals is the correlative of the Great Basin var. *Kingii*, but evidently does not, as is the case with var. *Kingii*, form a discrete population. For this reason it is deemed inadvisable to consider the bifid individuals as constituting a formally recognizable entity.

Type locality: Cokeville, Uinta County, Wyoming, June 11, 1898, *A. Nelson 4640* (Univ. Wyo.). The specimens of the type collections are quite intermediate between *A. capillaris* and the great body of material that has been known as *A. uintahensis*. In fact, particularly in the obtuse, merely cuspidate sepals, the type more resembles the former, *A. capillaris*. However, a collection, *A. Nelson 4583*, from Leroy, Wyoming, near the type locality and designated "cotype" on the University of Wyoming sheet (but not cited in the original description), is entirely characteristic of the population "uintahensis" in having sepals "narrowly ovate, acute" as designated in the original description. It must be assumed, therefore, that Nelson's diagnosis was drawn more largely from the Leroy collection and perhaps other representative material than from the type.

Distribution: Slopes and foothills to 8000 ft., southeastern Idaho and adjacent Wyoming, south in the Wasatch Range to Sanpete and Beaver Counties, Utah.

Representative specimens: Challis, Custer County, Idaho, June 6, 1935, *Smith 9*; Bush Ranch, Sweetwater County, Wyoming, June 10, 1900, *A. Nelson 7091*; Utah: Wasatch [Range], August 1869, *S. Watson 166*; Bear River Range, Cache County, June 9, 1936, *Maguire 13670*; Vernal, Uintah County, June 16, 1937, *Rollins 1745*; Maple Canyon, Moroni, Sanpete County, June 13, 1940, *Maguire 18671*.

ARENARIA KINGII subsp. **plateauensis** Maguire, subsp. nov. Caudicibus multicipitalibus; innovationibus frequentibus; caulibus (2) 5–10 (15) cm. altis, gracilibus, dense glanduloso-pubescentibus; foliis basilaribus (innovatiorumque) (0.5) 1.0–1.5 cm. longis, triquetribus, glabris mucronatis, minute serrulatis; foliis caulinibus 1–2 jugis (rare 3–4); inflorescentibus ab medio cauline, dense glandulosis; pedicellis (3) 4–6 (10) mm. longis, tenuibus; sepalis (3.5) 4.0–5.0 (6.0) mm. longis, lanceolatis, acutis vel aliquantum obtusis, moderate glandulosis; petalis (3) 4–6 (7) mm. longis, oblongo-oblanceolatis; glandibus 0.5–1.0 mm. longis, ovalibus; capsulis 4–6 mm. longis, ovato-oblongis; seminibus 1.5–2.1 mm. longis, papillatis, nigrescentibus.

The subsp. *plateauensis* is the eastern correlative of the western subsp. *compacta*, and has frequently been there referred. It has been most often interpreted as *A. aculeata*, however, with which it has no immediate affinities.

Type locality: Abundant, open park in spruce-aspen forests, Cedar Breaks rim, 10,400 ft., Iron County, Utah, June 23, 1940, *Maguire 19024*.

Distribution: Common in pine woodlands at lower altitudes and open aspen and spruce parks and ridges at higher altitudes, from 8000 to 11,500 ft., the high plateau region of south central Utah in Iron, Beaver, Garfield, Wayne, and Kane Counties, and in the Henry Mountains, Wayne and Garfield Counties.

Representative specimens: Utah: Frequent, spruce-aspen, 9500 ft., Aquarius Plateau, ½ mi. east of pass, 8 mi. east Widtsoe, Garfield County, June 27, 1940, *Maguire 19141*; common sage park, 10,000 ft., Aquarius Plateau, 2 mi. north Cyclone Lake, Powell National Forest, Garfield County, June 29, 1944, *Maguire 19233*; common, summit Mt. Ellen, 11,500 ft., Henry Mountains, Garfield County, July 2, 1940, *Maguire 19345*; common, meadow in spruce-aspen, 9000 ft., Big John Flats, Beaver County, July 19, 1940, *Maguire 19671*; Harris Flats, Kane County, July 4, 1937, *Gierisch 453*; Panguitch Lake, Garfield County, September 6, 1894, *Jones 6007*.

ARENARIA KINGII subsp. ROSEA Maguire, Bull. Torrey Club **72**: 326. 1946.

Type locality: Hilltop, yellow pine belt, Lee Canyon, 2600 m., Charleston Mountains, Clark County, Nevada, August 4, 1935, *I. W. Clokey 5560* (N. Y. Bot. Gard. Isotypes, Clokey Herbarium, Intermountain Herbarium).

Distribution: Known only from the Charleston Mountains by the type and the following collections: *Alexander 775a, 775b; Heller 11055*.

11. ARENARIA STENOMERES Eastwood. Leafl. West. Bot. **4**: 63. 1944.

Known only from the type collection: limestone cliffs, Meadow Valley Range, Lincoln County, Nevada, May 19, 1944, *Ripley & Barneby 3476* (isotype, N. Y. Bot. Gard.).

12. ARENARIA FRANKLINII Dougl. ex Hook. Fl. Bor. Am. **1**: 101. 1831.

A. Franklinii Dougl. ex Hook. β *minor* H. & A. Bot. Beechey Voy. 326. 1838.

Type locality: Snake County at Snake Fort, *Tolmie* sine no.

This plains species constitutes a relatively uniform population. A single variation in the var. *Thompsonii* Peck (Torreya **32**: 149. 1932) with bright green herbage and short (5–6 mm.) sepals is apparently known by only the type collection, *Thompson 4769*, from Gilliam County, Oregon. Specimens of the variety have not been studied, hence it is impossible at this time to arrive at any conclusion as to the proper status of the entity.

Type collection: Abundant on barren sandy plains and undulating grounds of the Columbia, from the "*Great*" to the "*Kettle Falls*," *Douglas* sine no. Probably at the British Museum.

Distribution: Sand and sage plains of the Columbia and Snake River drainages, Stevens County, Washington, south to Malheur (?) County, Oregon, and Owyhee County, Idaho.

Representative specimens: Connell, Franklin County, Washington, May 1902, *Elmer 2*; Soap Lake, Grant County, Oregon, June 15, 1935, *Thompson 11623*; Reynolds Creek, Owyhee County, Idaho, July 3, 1911, *Macbride 1016*.

13. ARENARIA HOOKERI Nutt. ex Torr. & Gray, Fl. N. Am. 1: 178. 1838.

KEY TO THE VARIETIES

Leaves mostly 0.3–1.5 cm. long.	*A. Hookeri* var. *typica*.
Leaves mostly 2–4 cm. long.	*A. Hookeri* var. *pinetorum*.

ARENARIA HOOKERI var. **typica** Maguire, var. nov.

A. Hookeri Nutt. ex T. & G. Fl. N. Am. 1: 178, as to type and major portion of population. 1838.

A. Franklinii var. *Hookeri* Rydb. Bot. Surv. Neb. 3: 27. 1894.

Type locality: Rocky Mountain range, on the summits of high hills (lat. 40°), *Nuttall* (not seen).

Distribution: Plains and exposed slopes and ridges mostly east of the continental divide, southern Montana, Wyoming, adjacent Nebraska, and Colorado. One collection, *Holmgren 1573*, from northeastern Elko County, Nevada, is typical of material from the natural range but for the longer sepals (8–10 mm. in length).

Representative specimens: Wyoming: Green River, Sweetwater County, June 23, 1896, *Jones* sine no.; Cheyenne, Laramie County, July 3, 1935, *Maguire 15906*, intermediate to var. *pinetorum*; Kemmerer, Lincoln County, July 11, 1935, *Maguire & Piranian 12354*.

ARENARIA HOOKERI var. **pinetorum** (A. Nels.) Maguire, comb. nov.

A. pinetorum A. Nels. Bull. Torrey Club 26: 350. 1899.

Type locality: Laramie Peak [Albany County], Wyoming, August 7, 1895 [*Nelson*] *1595* (Univ. Wyo.).

Distribution: Open pine and spruce woodlands, southeastern Wyoming and Colorado south to El Paso County, possibly through the range of the major population.

Representative specimens: Virginia Dale, Larimer County, Colorado, *Rollins 1797*; Colorado Springs, El Paso County, Colorado, May 29, 1878, *Jones 123*.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 1, PP. 57–59 JANUARY, 1947

LEAF VARIATION IN DELPHINIUM VARIEGATUM

HARLAN LEWIS

The conformation of the leaves affords one of the more conspicuous characters for the recognition of species in the genus *Delphinium*. Therefore, a study of leaf variation is of considerable interest. *Delphinium variegatum*, like all of the California representatives of this genus, is perennial. It forms a basal rosette of leaves during the late autumn, continues a limited growth through the winter, and produces a flowering stalk in the spring, whereupon, after fruiting, it dies back to the crown.

The leaves vary in the degree of lobing from the base of the plant to the inflorescence (fig. 1). Hence, an immediate difficulty arises as to the leaf that should be selected for comparison in quantitative studies. After careful observation it was concluded that comparable leaves can be obtained by selecting the uppermost leaf of the rosette (shown by x in fig. 1). During the past four seasons this leaf has been taken as a record from all of our plants. When, as is frequently the case, a plant has a branched crown with 2 or more flowering stalks, a leaf has been taken from each rosette. These we find are almost identical (fig. 2). If the plant is maintained in the garden for two or more seasons we have a leaf record of the same plant for different years.

The question arises: are the leaves chosen from a given plant in different years actually comparable? A plant which has a long growing season before maturing forms a dense rosette, whereas one which begins growth late in the season and matures early may form but a few leaves. In the first instance, we would be selecting perhaps the tenth leaf to be formed; in the latter perhaps the fifth. Hence, our comparisons might not be valid.

Our observations show conclusively that it is the position of the leaf with reference to the elongating stem that is of greatest importance in determining the morphology of the leaf, not its numerical position. The upper rosette leaves taken from different stalks of the same plant on the same year are remarkably similar regardless of the number of leaves in the rosette.

I wish now to call attention to the year-by-year variation. In figure 3 the upper row shows a series of upper rosette leaves taken in 1944 from 6 specimens of *D. variegatum* transplanted the previous year from a colony growing in San Luis Obispo County, California. The second row shows the comparable upper rosette leaves of the same plants taken in 1945. It can be seen that the leaves of each plant vary in the same direction, increasing in the amount of dissection. In some cases the difference between the leaves of

the same plant may be greater than the maximum difference between all of the leaves in 1944 (C–CC, D–DD).

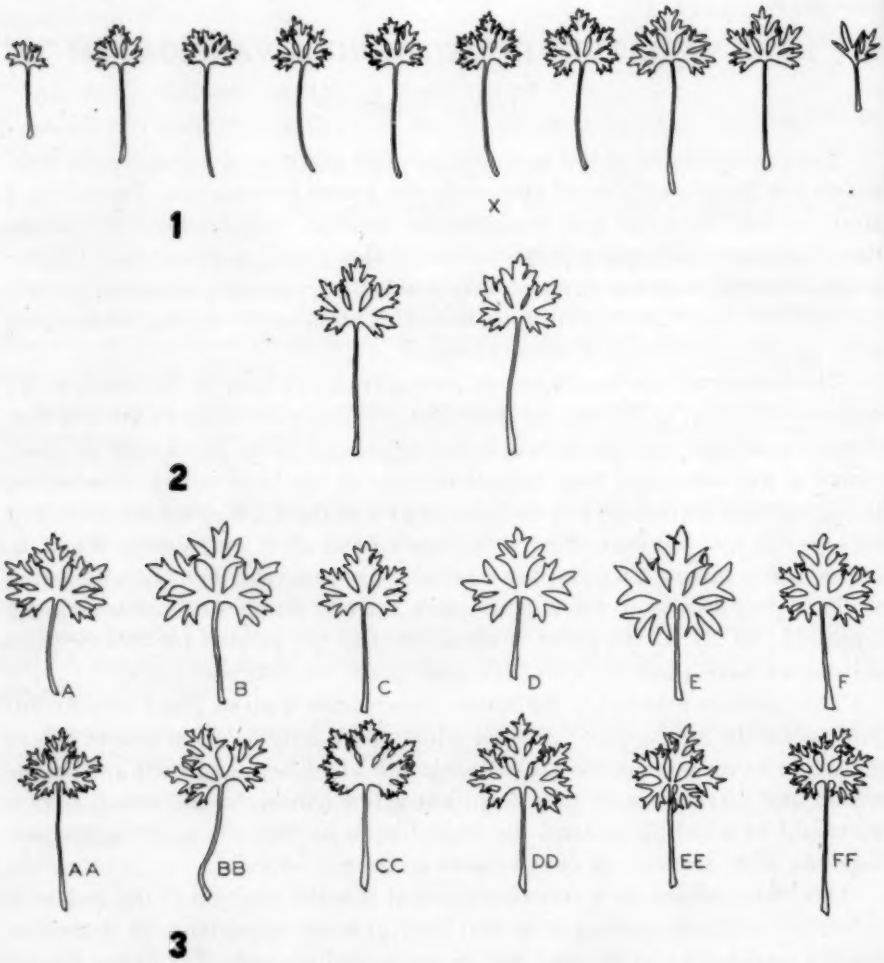


FIG. 1. The leaves produced by a plant of *D. variegatum* in one year. The lowest leaf is on the left, and the uppermost rosette leaf is indicated by x. FIG. 2. The uppermost rosette leaf taken from two stems of the same plant in the same year. FIG. 3. Uppermost rosette leaf of 6 plants from the same colony. Leaves taken in 1944 are indicated by single letters; corresponding leaves taken in 1945 are indicated by double letters.

All figures represent leaf tracings × ⅓.

Year-to-year variation of critical characters is a factor to be considered in studying the nature of variation of natural populations. The use of representative or mass collections in systematics for studying morphological variation has been much emphasized in recent years and has been used to con-

siderable advantage, particularly in the study of "complex" groups. In some cases the data have been suitable for the application of refined statistical techniques.

In view of the data just presented, it seems well to point out that the study of representative collections, no matter how intensively studied, may not yield as accurate an account of the variation as one perhaps would expect from the refined techniques that can be applied to such data. Certainly if the difference between comparable leaves of an individual in two successive seasons exceeds that of the leaves of all the plants in the same population in the same season, we are justified in describing that variation as no more than the range and nature of the variation for the population for the particular season chosen. The total variability of a population may, in fact, greatly exceed that indicated by a study made in one year. It may be argued that the range of variability in a population will remain constant, that is, that the same variability curve would be maintained from season to season but simply shifted in one direction or the other. Data are insufficient to demonstrate what is actually the case in *Delphinium*, but one certainly would not expect a change in any of the environmental factors to have an equal effect on every genotype; therefore, it is to be expected that the nature of the variation of a population may change from year to year, even when the same individuals are involved.

The inadequacy of the herbarium method in certain phases of systematic work has often, and justly, been pointed out. It is to be granted that there are many limitations in the use of herbarium material, one being that it is not representative of the species since there is frequently a disproportionate number of "abnormal" or exceptional individuals. However, in spite of its limitations, if a group is well represented in the herbarium, and the material is suitable for quantitative comparison, it may be possible to obtain from it more valuable information as to the nature and the range of variation of the species as a whole than if one relies only upon mass collections for his analysis, which may be much more limited with respect to space and time.

DIVISION OF BOTANY, UNIVERSITY OF CALIFORNIA
LOS ANGELES, CALIFORNIA

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, No. 1, pp. 60–76. JANUARY, 1947

TROCHODENDRON, TETRACENTRON, AND THEIR MEANING IN PHYLOGENY

LEON CROIZAT

Trochodendron and *Tetracentron*, two genera of the so-called "Ranales" endemic to the Far East, have recently been investigated from the standpoint of taxonomy, anatomy, palaeobotany, and phylogeny by a group of authors (A. C. Smith, Jour. Arnold Arb. **26**: 123. 1945; Bailey & Nast, ibid. 143; Foster, ibid. 155; Nast and Bailey, ibid. 267). The reader is referred to their contributions for the data and the bibliography not mentioned in these pages.

These same genera had received prior independent attention on the part of the present writer in the course of the preparation of two works of comprehensive scope, one devoted to the generalities of angiospermous dispersal, the other to an inquiry into the phylogeny of the seed plants. Of these works the former is in final manuscript and may be published in the not too distant future; the latter, on the contrary, is now unlikely ever to see the light. Considering that *Trochodendron* and *Tetracentron* are most interesting for the phylogeny of the flower, and of the higher plants as well, it seems advisable to place on record without delay observations which might otherwise be lost and will prove of service to coming students of these subjects.

The final conclusions reached by Nast & Bailey concerning these two genera are that, although conspicuously different in several respects, *Trochodendron* and *Tetracentron* are phylogenetically close. They believe that neither has near-kinship with families which might be supposed to lie in their vicinity, Eupteleaceae, Magnoliaceae, Himantandraceae, Winteraceae, Schizandraceae, Cercidiphyllaceae, and Eucommiaceae. The conclusions of these authors, consequently, are negative, and contribute nothing to our appreciation of the lines of evolution at work in this horizon of phylogeny, and to our ultimate understanding of the so-called "Ranales."

The subject now before the writer is vast, and could justify an extensive paper. This being impossible, the limited purposes of this review must be satisfied within the compass of (a) brief notes on the ovulation, geographical distribution, and sclereids of *Trochodendron* and *Tetracentron;* (b) a study of their floral structures, reduced to bare essentials. The purpose of the writer is to leave the subject under discussion in a state fit to promote its ready use in different branches of botany and to yield the important data of which it is readily capable.

THE OVULE AND SEED

Nast & Bailey believe (op. cit. p. 274) that the vascularized, sub-chalazal projections of the ovules and seeds of the two genera appear to be unique among the Angiosperms on account of the "hair-pin" turn taken by the raphe (Nast & Bailey's "funiculus" in op. cit. pl. 4, figs. 16, 17) before entering the chalazal plate. It is pertinent to remark in this connection that "hair-pin" turns of the ovule- and seed-vasculation quite, or very nearly quite, as pronounced as those of *Trochodendron* and *Tetracentron* occur in the Thymeleaceae (*Passerina filiformis;* Guérin, Ann. Jard. Bot. Buitenz. **29** [Sér. 2, 14] : pl. 1, fig. 2. 1916. *Wikstroemia indica;* Strasburger, Flora **100**: pl. 6. fig. 1. 1910), in the Rosaceae (*Vauquelinia corymbosa;* Juel, Svensk. Vetenskaps. Akad. Handl. **58**(5) : 47, fig. 81. 1918), and the Butomaceae (*Limnocharis emarginata;* Nitzschke, Cohn Beitr. **12**: 245, fig. 16. 1914).[1] A critical comparison made of these species with others in the same families (e.g., *Daphne striata, Kagenechia lanceolata, Butomus umbellatus*) or in other families (e.g., *Nepenthes;* Kühl, Bot. Centralbl. Beih. **51**(1) : 318, fig. 1. 1933) strongly suggests that these "hair-pin" figures arise, or are obliterated, even in related forms by the interplay of various secondary elements, the region of abscission of the seed, the length of the funiculus, the course of the raphe through the seed-coats, the degree of atrophy, more or less pronounced fusion of the ovular integuments. Peculiar trajects of the raphe moreover are well known in sundry families (Miers, Trans. Linn. Soc. **22**: 81, 97. 1856), and vascular "hair-pins" may seemingly be expected even in the arils or epimatia of certain conifers (*Podocarpus ferrugineus;* Sinnott, Ann. Bot. **27**: pl. 6, fig. 17. 1913, for example).

The peculiarities of the vasculation of the ovule and seed of *Trochodendron* and *Tetracentron*, consequently, cannot be stressed without regard to their homologies in families that have no phylogenetic ties with the Trochodendraceae. We are still poorly informed on the whole, but enough is already known to demonstrate that alate and exalate seeds with variable coats occur, for instance, in the Droseraceae (Wynne, Bull. Torrey Club **71**: 173, figs. 6, 9, 12. 1944) and the Nepenthaceae, the classification of which (Harms, Nat. Pflanzenf. **17b**: 756. 1936) is now based upon whether the seed is exalate, partly alate, or entirely alate. It is relevant for the purpose of this review that small, mostly alate seeds suggestive of *Trochodendron* and *Tetracentron*

[1] A perfect "hair-pin" turn in the vasculation of the funiculus, due this time to a failure of the ovule to assume its standard position, is illustrated by Leliveld (Rec. Trav. Bot. Néerl. **32**: 569, fig. 23. 1935) in *Ulmus hollandica.* Interesting considerations, here unfortunately out of place, are suggested by a comparison of this aberration with the irregular ovulation of another ulmaceous form, *Holoptelea integrifolia* (Capoor, Bot. Centralbl. Beih. **57** A: 233. 1937). Students of the morphology and phylogeny of the ovary will find most valuable material in the Ulmaceae, Moraceae, and Urticaceae. See also mention of the tubillus-like micropyle of *Leucosyke* in a coming page.

are found in the hamamelidaceous *Liquidambar* and *Bucklandia,* whether or not it be true that these seeds have vascular "hair-pins."

GEOGRAPHICAL DISTRIBUTION

The present distribution of these two genera is accounted for by A. C. Smith in much detail. They essentially belong to warm-temperate to temperate China or Japan. Bailey & Nast point out that their fossil record is extensive, dating back to the Lower Cretaceous and perhaps the Jurassic, and mention probable finds in the Rajmahal horizon of India. The two authors opine that these two genera or their immediate ancestors were once widely distributed in "Holarctica" but subsequently confined to a "relic" area in the Far East.

Trochodendron and *Tetracentron,* consequently, occupy a most critical range in dispersal, China and Japan being well known as two of the main phytogeographic centers of the world. The suggestion that they might have originated in "Holarctica" fits in nicely with the widespread belief, held among others by Berry (e.g., Geol. Soc. Am. Spec. Papers **12**: 32. 1938), that this mythical continent was the cradle of angiospermy.

A well rounded approach to the problem of dispersal requires the preliminary understanding of three main factors. (a) All life migrates along definite tracks, for no region was ever open to a lone genus or species. The writer does not agree in the least with Guppy's ultimate conclusions, but is fully satisfied that this author (*Plants, Seeds, and Currents in the West Indies and the Azores,* p. 332. 1917) is right when he acknowledges the deep impression made on him by the fact that forms so diverse as *Sphagnum* and *Carex* appear to migrate together. Likewise, the writer rejects Irmscher's generalities of interpretation as to dispersal, but does not doubt for a moment that certain dominant causes ("bewirkenden Ursachen"; Mitteil. Inst. Allg. Bot. Hamburg **8**: 364. 1929) mold the dispersal of all plants alike. (b) For the reason just given, it proves misleading to use any single group as standard to judge of tracks and dispersal, because phytogeography is of the earth at all times. (c) Isolated forms like *Trochodendron* and *Tetracentron* must be brought back to their phylogenetic center of origin before anything can be ventured on their first appearance and subsequent dispersal.

As will later be seen, the Trochodendraceae belong to the same archetypal node which released the Hamamelidaceae, Platanaceae, Nyssaceae, Cornaceae, and Saxifragaceae in a prior—when not in the very first—place. The Platanaceae are supposed to represent a classic instance of "holarctic" angiospermous origin, for *Platanus* is now wholly unknown in the southern hemisphere, being otherwise a very ancient form. Although often believed to be in the same case as the Platanaceae, the Hamamelidaceae are also, on the contrary, endemic both to Madagascar and Queensland, and, peculiarly,

enough, the genera so located, *Dicoryphe* and *Ostrearia*, appear to be related (White in Proc. Roy. Soc. Queensl. **47**: 61. 1936), which leaves the proponents of "holarctic" origins free to speculate, but unable to produce solid reasons for their assumptions. The Cornaceae, despite their being rife in the Northern Hemisphere, are an "antarctic" family in the narrow sense of the definition of Skottsberg (Plant World **18**: 129. 1915) because the genus *Griselinia* occurs both in Chile and New Zealand. Peculiarly again, the austral genus *Corokia*, traditionally received under the Cornaceae following Wangerin [Pflanzenr. **41**(4[229]): 92. 1910], has recently been transferred to the Saxifragaceae by Engler (Nat. Pflanzenf. **18a**: 215. 1930), which agrees with Hallier's understanding of its true affinities (Bot. Centralbl. Beih. **39**(2): 124. 1923). In Englerian classification *Corokia* falls in with genera endemic to the Mascarenes, Australia, Lord Howe Island, New Caledonia, and New Guinea, therefore of prevailingly "antartic" or "old oceanic" type of dispersal.

It is plain, consequently, that the Cornaceae and Saxifragaceae—not to mention other families here necessarily omitted—are bound by clear phylogenetic ties not to "holarctica" but to the southern hemisphere. This indeed is the case with an overwhelming majority of the angiospermous families, and the difficulties attending the theory of "holarctic" origin for genera like *Fagus* and *Nothofagus* are duly stressed by Wulff (Istor. Geogr. Rastenii: 525. 1944), who ultimately rejects Berry's conclusions (Plant World **19**: 68. 1916) as unfounded.

Allowing the matter to rest for the present, the writer emphasizes here the existence of a major track of angiospermy which, originating somewhere along the line New Zealand–Fiji, boldly sweeps forward through Malaysia, ultimately to reach at least the Far East and the Himalayas.[2] This track may suffer major disconnections also in Malaysia, but its outlines are readily discernible in the dispersal of certain "bipolar" species (e.g., *Carex Gaudichaudiana, Euphrasia* sp.; Du Rietz, Acta Phytogeogr. Suec. **13**: 215. 1940), and its inception indeed follows in the main the ancient shore so pointedly outlined by Bryan (Jour. Proc. Soc. New So. Wales **78**: 42. 1944) among other geophysicists. Interesting comparisons are suggested between this ancient shore and Skottsberg's map (Proc. 6th Pacif. Sci. Congr. **4**: 706, fig. 21. 1939) showing the eastern limit of a fairly rich orchid flora.

[2] The huge distributional gap in India, Afghanistan, and South-Eastern Persia which as a rule either chokes off altogether, or materially interrupts this track between the Burmese boundary and the Caucasus is suggested by the strongest evidence to depend in part upon aridity in the ranges mentioned. It is well known, for instance, that northern India has undergone desiccation even in historical times (Randhawa, Jour. Bombay Nat. Hist. Soc. **45**: 558. 1945), and that Indian ranges which man saw well covered with luxuriant evergreen tropical forests of probable "Malayan" affinities about twenty centuries ago are now sandy wastes rich in xerophytes of prevailing "African" origin.

In conclusion, the Trochodendraceae and Tetracentraceae are by no means "holarctic," and only a lack of appreciation of their phylogenetic ties, and a general disregard for the fundamentals of phytogeography may account for hasty assumptions, or implications, in this sense. They belong to the archetypal plexus of the Hamamelidaceae, Platanaceae, Nyssaceae, Cornaceae, and Saxifragaceae, and their origin is inextricably bound up with that of all these families, and with other families in this broad affinity. They are relics and isolated offshoots of ancestors which yielded swarms of genera and species in other directions, and, anticipating the publication of a coming work, the writer ventures to assert that the origin of all these families is to be sought unmistakably in the southern hemisphere, and most likely in the present case somewhere in the existing southwestern Pacific. Suffice it to say that a typic Sino-Himalayan family like the Lardizabalaceae has two genera wholly isolated in Chile, which should readily give pause to hasty speculations about the "holarctic" origins of forms now appearing as "relics" in the Far East.

THE SCLEREIDS OF TROCHODENDRON

The skillful handling of these bodies by Foster (Jour. Arnold Arb. **26**: 155. 1945; Am. Jour. Bot. **32**: 456. 1945) and his additional work on those of *Camellia* (Bull. Torrey Club **71**: 302. 1944) readily suggest to a critical reader that our understanding of sclereids is most imperfect in anything but certain readily observable facts. Considering that sclereids—or bodies supposed to be homologous with sclereids—occur in families so diverse as the Musaceae and the Theaceae, and that the details of their organization and origin are endless—witness the comments of Duval-Jouve on the crystals of *Sagittaria* (Acad. Montpell. Mém. Sci. **8**: 170. 1872) and the notes of Vöchting on those of *Myriophyllum* (Nova Acta Acad. Leopold. Nat. Cur. **36**: 1. 1873)—we might readily agree that the subject is not yet out of the descriptive and purely speculative stage.

Foster reports (Jour. Arnold Arb. **26**: 159. 1945) that sclereids are largely confined in the petiole of *Trochodendron* to the inner, highly lacunate cortical parenchyma. The ultimate significance of this localization may still be obscure, but an interesting suggestion to assist further basic research is perhaps to be found in the circumstance that septations in the foliage and stems of very many families (Duval-Jouve, op. cit.; Briquet, Bull. Herb. Boiss. **5**: 453. 1897) seem to represent, together with various types of "nodes," a region of election for sclereids and raphids.

Duval-Jouve's most interesting work follows the breaking down of these septate structures from the petiole into the blade, and it is a matter of regret that his material did not include *Hydrocleis nymphoides* of the Butomaceae which the writer believes to be peculiarly instructive. Duval-Jouve's contri-

butions makes it at least possible to conceive of a rational approach both to the problem of the sclereids and of septate stems and petioles, which appear to be to some extent interrelated, and, once suitably approached, may contribute much which is vital to a better understanding of the phylogeny and ontogeny of the angiospermous stem and leaf.

The writer believes that the students of sclereids will be amply repaid if they critically compare these bodies with the following structures: (a) permeable cells ("Durchlasszellen") in the exodermis of the roots of the Asclepiadaceae (Francke, Planta **3**: 1. 1927), and the so-called velamen of the roots of Orchidaceae and Araceae (Goebel, Flora **115**: 1. 1922); (b) hydropotes, so-called in many aquatics (Mayr, Bot. Centralbl. Beih. **32**(1): 278. 1915); (c) lithocysts in the Moraceae and their allies, not to mention other families (Renner, Bot. Centralbl. **25**(2): 183. 1910; Ajello, Am. Jour. Bot. **28**: 589. 1941); (d) "tracheids" and similar organs in many forms, from the Monocotyledons to the Cactaceae (De Fraine, Ann. Bot. **24**: 158. 1910).[3]

The writer ventures to believe that all these bodies and organs are at bottom structures which perform or performed the same functions either in storage or in assimilation, some of them still active, others on the contrary de-activated by the oncoming of entirely new secondary structures in the stem and the leaf. The ultimate origin of the vasculation of the higher plants might perhaps be sought in a critical investigation of these mysterious organs. Like several other fields of the utmost significance for pure and applied botany, the field of research here but roughly outlined is practically untouched, which is an excuse for the writer to speak of it as he does. We face here an interplay of form and metabolism which reaches most deeply into the problem of the ultimate origins and present morphology of the modern plant, and this interplay will forever escape us if we persist in approaching it along any front but the widest. Nature carries its own requirements, which it is for us to follow, not to modify nor to deny.

Clearly, Foster is correct in stressing our present lack of knowledge, and in questioning the very validity of standard definitions in current textbooks. Nothing can be concluded, of course from the presence of sclereids in *Trochodendron*, for there are too many families altogether unrelated to the Trochodendraceae which exhibit these organs; but their localization within

[3] *Salicornia* would seem to be peculiarly instructive in this connection. According to De Fraine (Jour. Linn. Soc. **41**: 331–334. 1913) "stereides" and "spiral cells" are in some measure interchangeable among different species under this genus. In *S. glauca*, for instance, there are "abundant stereides" around the vascular cylinder of the stem just below the nodal region, and also in the free leaf-tip, where "transfusion tissue" is located in the allied *Halocnemum strobilaceum*. Only stereides occur in *S. glauca*, but in other species, as *S. pusilla*, *S. ramosissima* etc., spiral cells exclusively appear. Both stereides and spiral cells, finally, are present in *S. fruticosa* and a few other species.

the spongy parenchyma of the petiole of *Trochodendron* is at least suggestive in the directions here but superficially indicated.

THE FLOWERS OF TROCHODENDRON, TETRACENTRON, AND THEIR ALLIES

Judged solely from the standpoint of the flower (figs. 1, 2) *Trochodendron* and *Tetracentron* appear to be unrelated. Sharp morphological differences separate these structures at a glance, nor is any suggestion readily forthcoming on how one has evolved into the other. Unmistakable evidence of ultimate kinship, however, is at hand from a sum of characters of positive and negative order, which proclaims that these two genera are united, after all, by common bonds of consanguineity.

The problem which these two genera offer is one which a systematist is frequently called upon to elucidate and to resolve. This problem invites in the first place a consideration of the flower in general, for its prime requirement is to ascertain the nature of the evolutionary trends, which, starting from a common ancestral form, ultimately cause different structures to come into being by gradual or abrupt modifications of their organs. The flower is one of the first standards of botanical investigations, if not the very first, and its pre-eminence endures throughout.

Common sense dictates that the flowers of *Trochodendron* and *Tetracentron* should be compared with the flowers of other forms which lie at the same horizon of phylogeny, in order to identify with reasonable accuracy the level of evolution which belongs to the two genera. Once this level is detected further constructive study becomes easy. It matters little indeed whether or not *Trochodendron* or *Tetracentron* are to be treated as members of this or that family or order, but it matters a great deal that they be properly placed and understood against the background of the evolutionary trends which they share.

Hallier pointed out (Bot. Centralbl. Beih. **14**: 247. 1903) that the Trochodendraceae and the Magnoliaceae are connected with the so-called Amentiferae through the Hamamelidaceae, and Solereder maintained (Ber. Deuts. Bot. Ges. **17**: 387. 1899) that the Trochodendraceae are related with the Hamamelidaceae through genera like *Cercidiphyllum* and *Eucommia*. Generally speaking, Hallier's work proves most confusing to all of its readers who are not already quite familiar with the groups to which this author summarily refers in the pages of his over-meaty treatments. Like Baillon's classification, Hallier's conclusions are not popular writing, and for this very reason, whether right or wrong, they seldom receive their dues. Solereder, of course, is best known as a wood anatomist, and is sought after as a purveyor of facts rather than as a full-fledged systematist.

Whatever be the ultimate merit of their contributions in certain details, both Hallier and Solereder are on record as having detected a measure of

kinship between the Trochodendraceae and the Hamamelidaceae. Horne believes (Trans. Linn. Soc. II. **8**: 239. 1914) that the Hamamelidaceae—which he calls "fairly homogeneous"—can be brought back for their origins to a "pro-Saxifragean plexus." This belief agrees in substance with Baillon's (Hist. Pl. **3**: 325. 1872) inclusions of the Hamamelidaceae, Platanaceae, and the like, within the Saxifragaceae. None of the literature here cited is reported by Nast & Bailey, who might be familiar with it, but seem to have accorded it no importance.[4] This rejection does not seem to be justified, for Hallier, Solereder, Horne, and Baillon had some knowledge of plant life, and Dutailly's obituary of Baillon (Bull. Soc. Linn. Paris **2**(No. 153): 1209. 1896) pointedly emphasizes that this master botanist, a man of wide culture and a lover of fine arts to boots, "fut de tous les botanistes qui ont vécu jusqu'à ce jour, celui qui tint dans ses mains le plus de plantes."

As a preliminary toward dealing with *Trochodendron* and *Tetracentron*, we may review somewhat briefly certain forms suggested as relevant to our purposes by the authors mentioned, such as *Liquidambar*, *Platanus*, *Davidia*, and the like. The reader is soon to perceive that the time so spent is quite as usefully employed as that devoted to peering through a microscope, if this peering is done without having effected a prior broad survey of the field of investigation that is ultimately to come under the binocular.

Liquidambar is variously treated as a genus of the Hamamelidaceae or Altingiaceae, which is here irrelevant, for, treated as any one may please, *Liquidambar* certainly belongs under the hamamelioid wings. Its flowers are coacervated within heads or balls which appear as the buds first unfold, the ♂ heads being usually borne above the ♀ within elongate rameal inflorescences.

These heads are developed either to maleness or femaleness, but the separation of the sexes, though fairly sharp on the whole, is seldom absolute. The female head contains a variable number of flowers each consisting of two carpels (rarely one) surrounded by a characteristic whorl or rings of scales which repeat their origin from the mass of the head below, or torus. The flowers are tightly crowded, so that the scales belonging to any one are hemmed in by those of the others. Along the commissural lines so formed appear glandular bodies with a tumid papillate head, very prominent at the

[4] The works of several authors, including those of Hallier and Solereder here cited, are indeed mentioned by A. C. Smith in his "Taxonomic review of *Trochodendron* and *Tetracentron*" (op. cit. 127) as having some historical significance. Of Hallier's phylogeny in regard to these genera, *Eucommia*, *Cercidiphyllum*, and *Euptelea*, Smith curtly states, "It is an opinion which has found no supporters and which is scarcely substantiated by the facts." It is a matter of regret that this dismissal is unsupported by a critical comment to demonstrate how the facts scarcely substantiate fruitful comparison of *Trochodendron* and *Tetracentron* with the Hamamelidaceae; the reader of these notes is now offered the opportunity to settle this for himself. Smith's assumption is ready proof that Hallier is all too often misunderstood.

time of anthesis, which are shown to be abortive stamens, or staminodia, by the fact that occasionally some of them shed pollen from well formed thecae. Whether staminodes of the same kind sometimes arise also between the embossed heads of the scale remains to be ascertained; at any rate, the scales, at first inconspicuous and hidden beneath the towering staminodes, develop as the head mature, and ultimate become manifest and woody. The ♂ head tends to elongate, unlike the ♀ which retains a sphaeric shape throughout.

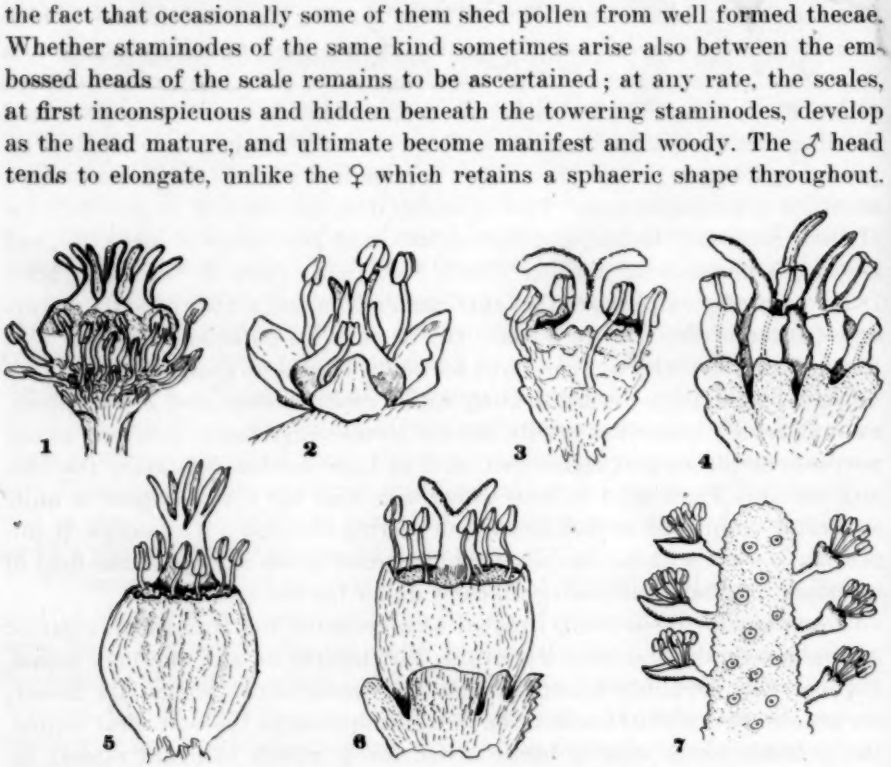


FIG. 1. A flower of *Trochodendron*. The glands on the back of the carpels are stippled. The numerous stamens are borne upon much reduced scales, and the whole is subtended by a pair of bracts. FIG. 2. A flower of *Tetracentron*. FIG. 3. A single flower of *Liquidambar* surrounded by scales bearing staminodes. FIG. 4. A single flower of *Platanus* (reduced to three carpels, each bearing a stamen dorsally). Staminodes are below the stamens, and the whole is surrounded by toral emergences or scales. FIG. 5. A flower of *Davidia*, the stamens set amid minute scales. FIG. 6. A flower of *Camptotheca*. The stamens are set around a tissue of glandular appearance. The outer "perianth" is surrounded by toral emergences or scales, usually inclosing more than one flower. FIG. 7. A diagram to show derivations from the purely ♂ inflorescence of *Davidia* (The florets facing the reader are supposed to be cut off). At the right actinomorphic perianths (quercoid type); on the left zygomorphic or scale-like perianths induced by dorsiventrality (myricoid type). (All figures diagrammatic.)

It contains very numerous stamens which appear to be set around wholly abortive carpels. While the ♀ head normally carries staminodes, even stamens, the ♂ inflorescence is seldom anything but unisexual.

A question that still requires investigation is in the ultimate origin of the staminodes or stamens of the ♀ head, whether they arise from toral tissues between the scales of adjacent flowers, or actually belong to the dorsal

(abaxial) surface of these scales. The matter is minor, for the scales themselves are from the body of the head, or torus, which is to say that the staminodes either belong to the scales that immediately surround the carpels, or to a row of subsidiary, undeveloped scales abaxially located from these. In this knowledge, and leaving details open for the present, a single flower from the ♀ head of Liquidambar may be figured in a manner (fig. 3) which answers both possibilities, and is basically acceptable for the purposes of this brief review.

The monotypic Platanaceae are notoriously allied with the Hamamelidaceae. The inflorescences of *Platanus* have been investigated by Brouwer (Rec. Trav. Bot. Néerl. **21**: 369. 1924) with startling results. While the flowers of this genus have constantly been accepted as actinomorphic, Brouwer shows that if there is any part of the balls of *Platanus* which may be called a "flower" this is a group constituted by a single stamen with a single carpel. These two sexual bodies are intimately connate and both receive derivations from the same ultimate vasculation. The stamen is much larger than the carpel, so large as a matter of fact that under certain conditions it appears to carry a basal ovule. In some cases the stamen is abortive, and the carpel then carries upon its back a staminode of more or less pronounced glandular nature.

A variable number of these sexual units, each consisting of a stamen, or staminode, and a carpel, are grouped in a pseudocyclic manner at definite regions of the head, which creates the illusion of actinomorphy. Certain heads are entirely ♂, others altogether ♀, many stamens being usually suppressed or reduced to staminodial condition. Heads evolving to maleness are usually located higher than those of the ♀ sex.

The heads or balls of *Platanus* are commonly believed to be connected by branch-like peduncles, but Brouwer shows that this, too, is an illusion, for each system or group of heads actually forms a single inflorescence, which consists of a central head surrounded by other heads arranged more or less in a spiral manner. Under each pseudo-flower in the head there is a slight projection from the torus which carries the stamen-carpel units in more or less regular whorls, and this projection is surrounded by an evascular scale, which Brouwer describes as a "proliferation of the ball" but illustrates most unfortunately in a manner which is not altogether clear. The purely ♂ or ♀ flower arises by abortion of one sex.

A false flower of *Platanus*, consequently, may be figured in the light of Brouwer's data in the manner here shown (fig. 4), which agrees with its conventional representations in the literature. The inflorescence itself, of course, is a peculiar thelome or phyllome (whichever be the term a reader may prefer, for the writer is not interested in standard definitions, and even less in coining and using new terms), reminiscent in some measure at least of the inflorescence of the moraceous (or urticaceous) genus *Cecropia*.

Davidia, a peculiar monotype credited either to the Cornaceae or Nyssaceae, has been carefully studied by Horne (Trans. Linn. Soc. II. **7**: 303. 1909) both as to general and floral anatomy. It is a matter of regret that nothing can be said here of the anatomy of the seedling, which is of the utmost interest for various fields of interpretive botany. As for the inflorescence, this consists of a globular head, subtended by two conspicuous bracts, which earned for this genus its common name "dove tree." This head contains very numerous ♂ flowers, and a single zygomorphic ♀ flower, which might properly be called bisexual on account of the presence of a certain number of stamens, as it will soon be stated.

The stamens of the ♂ part of the head are very numerous, and are clustered at first in groups within depressions of the torus, or foveolae. Later these foveolae are lifted by toral growth so that they form minute cups with short pedicels. The prevailingly ♀ flower, at first hidden within the mass of the purely ♂ part of the head, next emerges from a low pedicel. This flower has no "perianth," but carries about 15–26 stamens at the base of the compound style, which stamens appear between bodies described as "exceedingly minute excrescences" by Horne. The ovary is of 6–9 carpels basally fused, and the single ovule in each carpel is fed by vasculation streaming in from the adjacent septa. The stamens of the prevailingly ♀ flower are serially arranged in an oppositilocular manner.

Leaving out of reckoning the purely ♂ part of the inflorescence, which is amply illustrated by Horne and other authors, the bisexual flower of *Davidia* may be figured in the manner here shown (fig. 5).

Camptotheca is another genus of the Nyssaceae or Cornaceae close to *Davidia*. The flowers are sometimes ♂ by abortion, so far as the writer has been able to ascertain, but do not differ in essentials from the seemingly bisexual ones (Hu, Ic. Pl. Sin. **1**: pl. 41. 1927), one of which is represented here (fig. 6). So far as is known to the writer, these flowers are borne in pairs upon a head or ball, and are surrounded at the base by a variable number of scales emerging from the head as toral outgrowths.

Strictures of space make it impossible to enter into details in this review, and the reader is referred to the works cited for much additional information. Beyond question, other data of considerable significance will repay the efforts of acute investigators who in due course turn their attention upon the genera and forms here dealt with, critically investigating them on a broad comparative front. As the evidence reads which is now available, however, several conclusions are indicated as necessary.

The first and most important conclusion is that these genera, understood as a whole, lie at that cross-road of evolution where amentiferous forms easily become perfect-flowered. To illustrate the point, let us take for example the

inflorescence of *Davidia* and break it into its two essential parts, ♂ and ♀. The ♂ part of this inflorescence becomes a head or ament upon which the individual flowers, borne actinomorphically or zygomorphically, are of a pattern which suggest (fig. 7) either the Myricaceae or the Fagaceae. The ♀ flower, shorn of its stamens, would be close indeed to that of *Castanea*, and, characteristically (Tognini, Atti Ist. Bot. Pavia, Nuova Ser. **3**: 1. 1894), *Castanea*, too, often carries stamens disposed precisely like those of *Davidia*. It is also clear that a prevailingly ♀ flower of *Liquidambar*, shorn of its staminodes, has the basic outline of a ♀ flower of *Juglans* (fig. 8), which consists of paired carpels, inclosed within scales. Characteristically once again, the scales of *Juglans* and its allies (C. De Candolle, Ann. Sci. Nat. Sér. 4 **18**: 5. 1862) may evolve in maleness, yielding bisexual flowers. All this is of course less than surprising, for, as Brouwer indicates, the basic constituent elements of all these flowers are emergences or scales which readily evolve in the direction of maleness or femaleness, or become abortive as staminodes and perianth-appendages of potentially undefined status. A glance at Eichler's classic diagrams (Blüthendiagr. **2**: 36. 1878) reveals that the scales evolving in full femaleness, or carpels, may take different positions in regard to the subtending bracts and axes in various juglandaceous genera. As a matter of fact, aberrant fruits of these genera are known to all keen students of plant-life, in which sterile loculation shows up, sometimes in very regular patterns, leading these students to infer rightly that the fruit of the walnut was originally a head of congested carpels within an undetermined number of scales.

In short, the vexed question, how and when the amentiferous plants become possessors of actinomorphic bisexual flowers is easily and readily answered along the lines just suggested. The sexuality of the so-called Amentiferae is definite as a rule in one direction only, though stamens or staminodes are by no means of rare occurrence in *Castanea*, and not uncommon in the ♀ flowers of other genera in that group. *Liquidambar, Platanus, Davidia, Camptotheca* are in active evolution away from the amentiferous stage, still retaining the head- or ament-like inflorescences and an ambiguous sexual expression, which leads on occasion to purely ♂ or ♀ heads or flowers.

The second conclusion is that, broadly speaking, the passage between flower and inflorescence, despite endless variants *of detail*, is at bottom anything but speculative and fraught with the difficulties which the literature contains. A fruit of the hamamelidaceous *Rhodoleia Championii* (Harms, Nat. Pflanzenf. **18a**: 335. 1930) suggests to the unwary a structure wholly homologous to a head of *Liquidambar*. However, if the flower itself be dissected, it will readily be learned that this flower consists of a variable number of bicarpellate ovaries (usually 5–6, occasionally 1, as shown by Harms)

fitted abaxially (fig. 9) with stamens[5] and conspicuous petaloid staminodes. The sepals are "concrescent," according to Harms, but could as well be described as toral emergences, for they belong not to individual ovaries but to the whole of the flower, which is in reality exactly intermediate between a true flower and an inflorescence. Naturally, if this peculiar structure be loosened up, as it were (fig. 10), and each ovary surrounded by stamens and petals (staminodes) throughout, a string of perfect bisexual flowers would appear to be compared with those of the Hamamelidaceae having absolutely actinomorphic bisexual perianths, *Fothergilla* or *Hamamelis* for example.

The third and last conclusion suggested here by these all too short considerations is that morphologists and anatomists who are not familiar with plant life in general often argue nugatory issues, mistaking their own definitions for something that nature wills but in reality abhors. Whether the ovule be "axile" or "borne upon the margins of the carpellary leaf," for example, is an issue which no one may take seriously who knows that within the closed chamber of an ovary less than 5 millimeters broad, for instance, vascular connections may take circuits quite as variable as those appearing in the ovule itself, and that "axile" and the "foliar" at this point are figments. Indeed, some ovules may be "axile," as those of the Araceae (Campbell, Ann. Bot. **14**: 20. 1900), but it is probable, as this author admits, that even in this family forms can be detected in which the ovules are borne on the "carpellary leaf." The issue is here with variants of which many are possible and probable, and variants of the kind are meaningless in the face of the basic realities of flower-structure and flower-phylogeny. Ink has flown in torrents to debate the origin of the stigma as something involved and mysterious, but in the Urticaceae, for instance, we find the seed coat (*Leucosyke capitellata*, fig. 11; Fagerlind, Svensk Vetenskaps. Akad. Handl. **21**(4): 11, fig. 2, b. 1944) produced into a so-called tubillus of *Ephedra* flavor. Contrariwise, the origin of the stigma need not worry us at all in a case like that

[5] The descriptions of nearly all the forms mentioned in this review are indifferent or poor in the literature now current. This is understandable, considering that the flowers of these genera cannot be interpreted in the light of the inadequate concepts of floral morphology commonly accepted today, witness the basic misinterpretation of the vasculation of the flower of *Trochodendron* by Nast & Bailey later documented in these pages. Harms' treatment of the Hamamelidaceae is unusually good from the descriptive standpoint, but a slight inconsistency appears in his handling of *Rhodoleia*. Harms' description correctly reports that staminodes (petals) and stamens fully evolve only around the outer (abaxial) side of the dimerous ovaries, and are rudimentary or altogether missing elsewhere, but the figure that illustrates the genus (op. cit. p. 335, fig. 175 C) appears to belie the description. It seems probable that this figure does not correspond to the truth, as the writer learned by actual dissections which confirmed Harms's diagnosis. It should be added, however, that these forms are so variable in details that departures from the norm are anything but impossible, and only abundant material may help to settle every detail with finality. Cleancut concepts, consequently, count far more in interpreting these forms than preoccupations with the fact that stamens fail on occasion to become petaloid, or that rudimentary staminodes turn up where none at all are supposed to occur.

of *Coleanthus subtilis* (Schnarf, Vergl. Embryol. Angiosp. 267. 1931), for a pollen grain falling anywhere on the lips of a carpel of this kind (fig. 12) will readily find its way to the micropyle by simply sending its tube downward. Since a leaf often ends in a secretory hydathode, it is not surprising

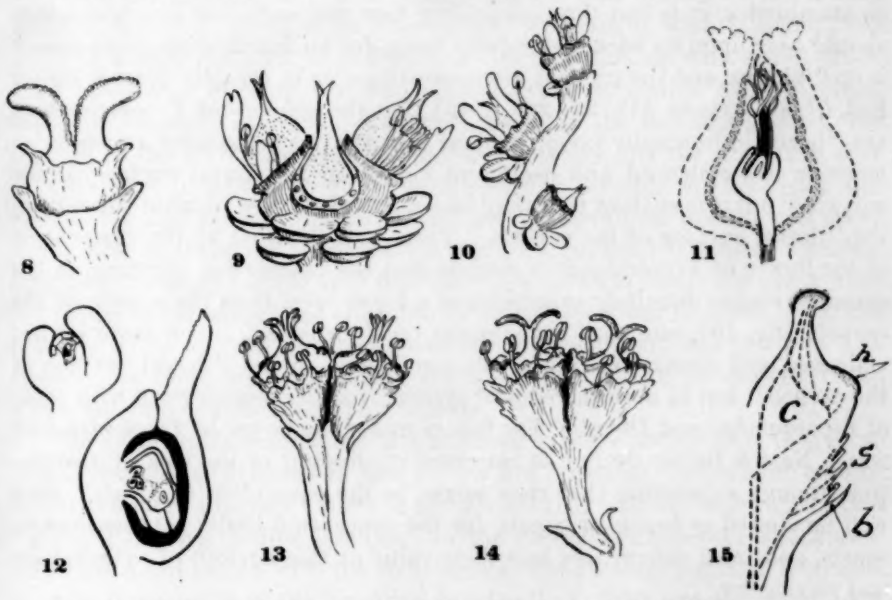


FIG. 8. A ♀ flower of *Juglans*. FIG. 9. A flower of *Rhodoleia Championii* (reduced to three 2-carpellate ovaries). The ovaries are set within a head, and embraced at base by its emergences which give origin to stamens and petals (staminodes) in an abaxial (outer) position. The "sepals" (lowermost tiers) as toral emergences common to the whole head, which they surround. FIG. 10. Fully *actinomorphic* hamamelidaceous flowers (type of *Hamamelis* or *Fothergilla*) derived from an elongation of the head of *Rhodoleia Championii*. FIG. 11. Young ovary of *Leucosyke capitellata* (adapted from Fagerlind, as cited in text), showing the tubillus-like extension of the inner ovular tegument. The region stippled is the inner layer of the carpels. Were this region only extant, this ovary would be structurally and functionally quite akin that of the Ephedraceae. FIG. 12. Upper left: Very young ovary of *Coleanthus subtilis* (Gramineae); lower right: The same fully developed (adapted from Schnarf, as cited in text). FIG. 13. Diagram to show two flowers of *Trochodendron* brought together within a single head. FIG. 14. Diagram to show two flowers of *Liquidambar* arranged like those of *Trochodendron* in figure 13. FIG. 15. Vasculation of the flower of *Trochodendron* (adapted from Nast & Bailey, as cited in text). *c*, body of the carpel; *h*, the dorsal gland with convergent suggestive vasculation; *s*, the staminal region and its ridges; *b*, the subtending bract. (All figures diagrammatic.)

that a carpel may end with a similar structure, and that the pollen should find this structure, usually rich in sugar and starch, convenient.

A flower of *Trochodendron* (fig. 1) hardly differs from one of *Liquidambar* (fig. 3) when both are critically examined, for the structural essentials are the same in both, despite the greater number of carpels in the former.

Supposing that two flowers of the former are bunched together (fig. 13) it is not easy indeed to find how they differ from two flowers of the latter (fig. 14) arranged in the same manner. Considering that the basic unit in all these flowers is the pair of scales evolved in maleness and femaleness, or sterilized as staminodes, it is less than surprising that the carpel of *Trochodendron* should bear upon its back a glandular body, for an homologous development is in *Platanus*, and the stamens are oppositilocular in *Davidia*. Nast & Bailey find (Jour. Arnold Arb. **26**: 269. 1945) that the stamens of *Trochodendron* are "borne individually upon cushions that tend to be linearly arranged on more or less embossed and decurrent ridges on the dorsal surface of the carpels," but it is evident that they take a mistaken view of what constitutes the "dorsal surface of the carpels." Their own drawing of the vasculation of the flower of *Trochodendron* reveals that the vasculation abutting on the staminal region definitely originates at a lower level than the supply of the carpels (fig. 15), and that the stamens on "cushions . . . on more or less embossed and decurrent ridges" do not belong to the "dorsal surface of the carpels" but to a much reduced system of scales, homologous with those of *Liquidambar* and *Davidia*. The bracts under the flower of *Trochodendron* which Nast & Bailey decline to interpret on account of the lack of vasculation, though suggesting that they might be the equivalent of a calyx, may well be viewed as bracts or sepals, for the conceptual limits between bracts, sepals, and toral emergences lose their value at this horizon of morphology and phylogeny.

Considering that *Liquidambar* coexists under the Hamamelidaceae with *Hamamelis* and *Rhodoleia*, it is not difficult to understand how *Trochodendron* and *Tetracentron* are consanguineous despite the differences in their flowers. The same potential of evolution which yields the flower of *Rhodoleia* from that of *Liquidambar* is fit to yield that of *Tetracentron* from that of *Trochodendron*, for all these genera and flowers lie at one and the same evolutionary level. Space forbids to enter into minute details, but reference to the notes given for *Rhodoleia* may guide the reader to form his own conclutions about these details.

In short, *Trochodendron* and *Tetracentron* are isolated offshoots of a truly colossal phylogenetic plexus which is responsible for the evolution of the Hamamelidaceae, Cornaceae, and Saxifragaceae as the main families. The "Ranales" are a pure figment, for, narrowly understood, they must be restricted to forms having numerous stamens in a cyclic arrangement and heads of carpels; that is to say, the Ranunculaceae and Magnoliaceae in the main. Unduly enlarged to include the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, and the like, which hark back to a line of evolution entirely at variance with that of the Ranunculaceae and Magnoliaceae, the "Ranales" are meaningless, because *Platanus* and *Davidia* then become

"Ranalian," quite as much as the humble buttercup and the showy peony are.

DISCUSSION

The trend strongly active in botany against that branch of the science which is hazily referred to as "taxonomy" is fraught with mischief. The study of botany has been, is, and forever will be bound up with a well-diversified knowledge of plant life, and specialized investigation which neglects broad preliminary surveys of its chosen field, on the specious ground that surveys of the kind may be dispensed with, merely fills the literature with data which only those may really interpret who are able to effect such surveys in the first place. The herbarium and the botanical garden still stand as the first instruments of competent and well rounded botanical teaching, and students taught at the very first only that which is *inside* the plant without being at the same time educated to an appreciation of what is *outside* (that is, form and its corollary, potential of evolution) are fated to ultimately lose their bearings among the incredible wealth of evolved forms which enlivens plants in all their aspects.

The unfavorable results of a lack of broad surveys preliminary to specialized investigation detected in this review are apparent throughout botany. When Wetmore suggests (Torreya **43**: 21. 1943) if only by implication, that "certain seeming cauline bundles" in the cactus *Trichocereus Spachianus* may have a connection with the structures at the growing point of *Hippuris*, he fails to notice that the "cauline bundles" of *Trichocereus* (Boke, Am. Jour. Bot. **28**: 656. 1941) are unknown in another cactus, *Opuntia cylindrica*, also studied by Boke in the same paper. The reason for this difference is indeed simple. *Trichocereus* is wholly leafless, while *Opuntia* is not so; therefore the vasculation which should normally originate from, or abut on, the leaf of *Trichocereus* remains "cauline" of necessity. In certain succulents at least (e.g., *Salicornia;* De Fraine, Jour. Linn. Soc. **41**: 317. 1913) the whole of the outer cortex is foliar in origin, so that vasculation in the cortex of a leafless succulent like *Trichocereus* does not suggest a profitable field of comparison with the "cauline" vasculation of the growing tip of such other form as *Hippuris*, this genus lying wholly outside the morphological and phylogenetic field of *Trichocereus*. A proper survey of the matter indicates that *Hippuris*, a "microphyllous" genus, should be critically compared in the first place with its next of kin in the taxonomic and systematic sense. *Gunnera* takes first place among the genera to be investigated in relation to *Hippuris* and its typical growing point (Louis, Cellule **44**: 87. 1935), for it is closely allied with *Hippuris*, as a glance at Engler & Harm's *Syllabus* immediately reveals. Unlike *Hippuris*, however, *Gunnera* is a typical "macrophyllous" form. Its stem is quite as deeply dissected by the foliar traces as that of the Pteridophytes (Merker, Flora **72**: 211. 1889), but the ancient

"microphyllous" foliage of the ancestral form presumably common to it and *Hippuris* survives in the shape of peculiar bracts well illustrated by Skottsberg (Svensk. Bot. Tidskr. **22**: 392. 1928). Here, then, are subjects of investigation which handled under competent guidance not only promise results of the greatest importance as to the nature of the growing point of the Angiosperms, but herald most fruitful comparisons with the foliar differences among seedless plants, which Jeffrey wished to be fundamental (Anat. Woody Pl. 244. 1917) in obedience to dicta that answer only an anatomist's dreams. To compare *Hippuris* and *Trichocereus* on the strength that presumably "cauline bundles" belong, or might belong, to both genera leads simply nowhere.

SUMMARY

Implementing and correcting previous work written by various authors on two supposed "Ranalian" genera, *Trochodendron* and *Tetracentron*, the writer shows that these two genera are ultimately allied with the broad hamamelidoid-saxifragoid plexus as isolated forms. He briefly discusses their dispersal, ovulation, and floral peculiarities, and the sclereid problem. Incidental notes are offered on the phylogeny of the flower in general, and it is concluded that specialized investigation falls wide of its goals when it is dissociated from broad surveys preliminary to study.

THE ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, No. 1, pp. 77–80 JANUARY, 1947

NOTEWORTHY PLANTS OF SOUTH AMERICA—III. SPECIMENS OF MAURIA[1]

FRED A. BARKLEY

Among recent specimens studied were a series of eight collections of *Mauria*, representing for the most part species poorly represented in American herbaria or undescribed species.

Four of the specimens seem referable to described species: *J. Cuatrecasas 11370* (27 Dec. 1940, márgines del Río Mocoa, 570 m. alt., Comisaría del Putumayo, Colombia, in Herb. U. S. Nat.) and *J. Cuatrecasas, R. E. Schultes & E. Smith 12341* (17 Oct. 1941, 1300 m. alt., región del Sarare, Departamento Norte de Santander, Cordillera Oriental, Colombia, in Herb. U. S. Nat.), are *Mauria suaveolens* R. & P. Agreeing very closely with the original description and photograph of the type of *Mauria birringo* Tulasne is the specimen *A. Dugand & R. Jamarillo 2952* (1500 m. alt., 4 May 1941, arribe de "El Colegio," vertiente occidental de la Cordillera Oriental, Departamento de Cundinamarca, Columbia, in Herb. U. S. Nat.). *Delgado 43* [Mar. 1937, "arbol de 10 a 12 m de altura," silvas del Avila, Venezuela, in Herb. C. N. H. (Field) M.], is *Mauria heterophylla* H.B.K.

Four of the specimens appear to represent undescribed species.

Mauria Killipii[2] Barkley, sp. nov. Arbor 3–4 m. alta; ramis paucis, lenticellis prominentibus, striatis, dense ferrugineo-tomentosis vel cinarescentibus glabris; foliis pinnate 3-foliolatis, circa 10 cm. longis; petiolis crassis, circa 20 mm. longis, pilosis; foliolis lateralibus 2–4 mm. petiolulatis, foliolis terminalibus 6–12 mm. petiolulatis, petiolulis dense pilosis; foliolis membranaceis, utrinque prominente reticulata-nerviis, supra glabris, infra ferrugineo-tomentosis ad nervum, ovatis vel late lanceolatis, ad apicem acutis vel subacutis, ad basem late cuneatis, marginibus integris; paniculis axillaribus terminalibusque folio aequilongis; pedunculis sparse pilosis; bracteis deltoidis, sparse pilosis, ciliatis, subacutis, 1–1.5 mm. longis, subpersistentibus; calycibus circa 1.5 mm. diametro, lobis 5, late deltoideis vel late rotundo-deltoideis, sparse pilosulis, ciliatis, circa 0.3 mm. longis; petalis 5, ovatis, glabris, circa 1.3 mm. longis; staminibus 10, circa 0.45 mm. longis, antheris rotundis, flavis, circa 0.3 mm. diametro.

Tree 3 to 4 m. high, few branched and with straight trunk; branchlets yellowish brown with prominent lenticels, striate, at first ferrugineously pilose but soon glabrate; leaves pinnately 3-foliolate, about 10 cm. long; petiole coarse, about 20 mm. long, pilose; lateral leaflets short-petiolulate

[1] Publication is assisted by a contribution from the author.

[2] For Ellsworth P. Killip.

with petiolules about 2 to 4 mm. long, terminal leaflet petiolulate with petiolules about 6 to 12 mm. long, petiolules densely pilose; leaflets thinly membranaceous, with a reticulum of veinules showing prominently, glabrous above, the veins and venules below ferrugineously pilose, ovate (or rarely the terminal only broadly lanceolate), acute or subacute at apex, broadly cuneate at base, margin entire; inflorescences terminal thyrsus and lateral panicles; peduncle, rachis and branches of inflorescence sparsely pilose; bracts deltoid, sparsely pilose, ciliate, subacute, 1 to 1.5 mm. long, subpersistent; calyx about 1.5 mm. in diameter, calyx lobes 5, broadly deltoid to broadly rotund-deltoid, sparsely short appressed pilose, ciliate, about 0.3 mm. long; petals 5, ovate, greenish, glabrous, about 1.3 mm. long; stamens 10; filaments filiform, about 0.3 mm. long; anthers rotund, yellow, about 0.3 mm. in diameter; stigmas 3.

PERU: thickets and open woods, alt. 1800 to 2400 m., Huacapistana, dept. Junín, June 5–8, 1929, *E. P. Killip & A. C. Smith 24182* in Herb. C. N. H. (Field) M. 616242, TYPE.

This species resembles *Mauria ovalifolia* Turcz. in the character of the inflorescence. It appears to be most closely allied to *M. sericea* Loes. from which it differs in several minor details but from which it may at once be distinguished by the very much smaller inflorescence and the five to seven leaflets in *M. sericea*.

Mauria Cuatrecasasii[3] Barkley, sp. nov. Arbor circa 8 m. alta; remulis crassis, striatis, dense ferrugineo-pilosulis; foliis impari-pinnatis 6-jugis, circa 45 cm. longis, dense ferrugineo-pilosis, foliolis supra sparse pilosis vel subglabratis; petiolis circa 9 cm. longis; foliolis membranaceis, 9 mm. petiolulatis, anguste ovatis, integris, acuminatis, ad basem cuneatis vel late cuneatis et decurrentibus, 35–45 mm. latis, 80–130 mm. longis; paniculis axillaribus, crassis, pilosis; bracteis deltoideis, caducis; lobis calycis deltoidis, glabris; drupa ovoidea, circa 7.5 mm. longa.

Tree to 8 m. high; branchlets thick, striate, densely ferrugineously short pilose; leaves imparipinnately compound, about 45 cm. long, densely ferrugineously velvety-pilose throughout except upper surface of leaves sparsepilose to subglabrate; petiole about 9 cm. long; leaflets about 13, membranaceous, short petiolulate with petiolules about 9 mm. long, narrowly ovate, entire, acuminate, at the base cuneate to broadly cuneate and decurrent on the petiolules, 35 to 45 mm. broad, 80 to 130 mm. long; panicles axillary, coarse, pilose; bracts deltoid, caducous; calyx lobes deltoid, glabrous; fruit ovoid, about 7.5 mm. long.

COLOMBIA: "palo Hernández," 200 m. alt., Cuesta de Fusagasugá, Dept. Cundinamarca, 18 II 1940, *J. Cuatrecasas 8062* in Herb. U. S. Nat. 1796044, TYPE.

This species shows affinities to *Mauria ferruginea* Tul. from which it differs in having much longer leaves, membranaceous leaflets, and a less dense white pilosity which is not confined to the nerves and veinlets. It more closely resembles *M. sericea* Loes. which has subsessile, acute leaflets with prominent veinlets and with ferrugineous pilosity in that species confined to the midrib, nerves, and veinlets on the under surface.

[3] For J. Cuatrecasas.

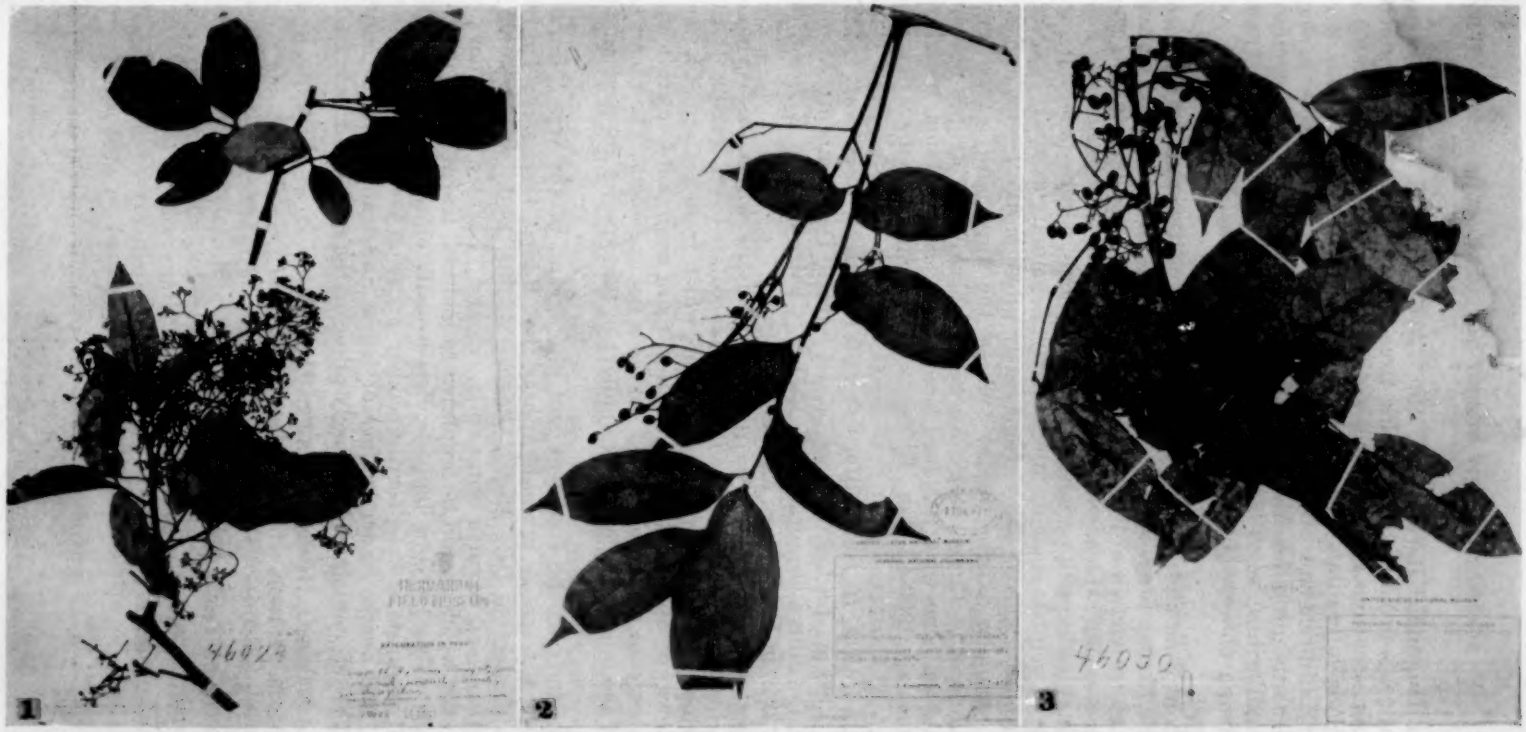


FIG. 1. Type sheet of *Mauria Killippii* Barkl., Huacapistana, Peru, 5–8, June 1929, *Killip & Smith 24182* in Herb. Chic. Nat. Hist. (Field) Mus. 616242. FIG. 2. Type sheet of *Mauria Cuatrecasasii* Barkl., Departamento Cundinamarca, Colombia, 18 February 1940, *Cuatrecasas 8062* in Herb. U. S. Nat. 1796044. FIG. 3, Type sheet of *Mauria Dugandii* Barkl., Departamento Cundinamarca, Colombia, 26 January 1944, *Garcia-Barriga 11021* in Herb. U. S. Nat. 1852216.

Mauria Dugandii[4] Barkley, sp. nov. Arbor circa 3 m. alta; ramulis crassis, lenticellis prominentibus; foliis circa 25 mm. longis, imparipinnatis, 2–3-jugis, senescentibus glabris, foliolis subtus exceptis; petiolis circa 6.5 cm. longis; foliolis lateralibus 2 mm. petiolulatis, foliolis terminalibus 2 cm. petiolulatis, elliptico-lanceolatis, nervis lateralibus atque venis utrinque dense reticulatis prominentibus, subtus valde caduce ferrugineo-pilosis; paniculis axillaribus, sessilibus, sparse pilosis, 6–12 cm. longis; bracteis caducis; drupa oblique oblongo-ovoidea, circa 10 mm. longa, 6 mm. lata, 3 mm. crassa.

Tree about 3 m. high; branches thick, brown, with prominent lenticels; leaves about 25 mm. long, imparipinnately compound, glabrate at maturity except for under surface of leaflets; petiole about 65 mm. long, leaflets about 5, subcoriaceous, lateral leaflets short-petiolulate with petiolules about 2 mm. long, terminal leaflet with petiolule about 2 cm. long, elliptic-lanceolate, with a reticulum of veinlets showing prominently, acuminate at apex, cuneate to rounded at base, glabrous above, fugaciously pilose on the nerves and veinlets below; panicles axillary in the axils of the uppermost leaves, sessile, sparsely pilose, 6 to 12 cm. long; bracts soon deciduous; drupes obliquely oblong-ovoid and somewhat flattened, about 10 mm. long, 6 mm. broad, red.

COLOMBIA: alt. 1900–2100 m., El Tablazo entre Subrachoque y San Francisco, finca "El Carmero," San Francisco Córdillera Oriental, Dept. Cundinamarca, 26 I 1944, *H. García-Barriga 11021* in Herb. U. S. Nat. 1852216, TYPE; alt. 1300 m., La Cabuya, región del Sarare, Departamento Norte de Santander, Cordillera Oriental, 14 X 1941, *J. Cuatrecasas, R. E. Schultes & E. Smith 12207* in Herb. U. S. Nat. 1850916.

This species resembles *Mauria puberula* Tulasne which has coriaceous leaflets, rachis, pilose, and long acuminate, lanceolate-ovate leaflets. It more closely resembles *Mauria ferruginea* Tulasne, which from a study of a photograph of the type appears to have smaller, more acuminate, ovate leaflets, and the pubescence of the rachis and petiole is not fugacious. The rachis and branches of the inflorescence (much smaller) of that species are permanently pilose.

From a study of the fragment and photograph of the type (*Karsten*, prov. Bogota, Colombia), it would appear that *Mauria ferruginea* Tul. var. *obtusifolia* Engler (in DC., *Monog. Phaner.* **4**: 331. 1883) would be better treated as a species, **Mauria obtusifolia** (Engler) Barkley comb. nov., the description for which should be amplified to include: leaves simple (above) to 7-foliolate, 67 to 130 mm. long; leaflets broadly elliptic, obtuse at apex, very broadly cuneate at base, ferrugineously pilose on young branches, petiole, rachis, and on the under surface of leaves and leaflets on the midrib, nerves, and veins; panicle small, densely pilose on the rachis and its branches.

CHICAGO NATURAL HISTORY MUSEUM HERBARIUM
CHICAGO, ILLINOIS
AND
UNIVERSITY OF TEXAS HERBARIUM
AUSTIN, TEXAS

[4] For Armando Dugand G.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, No. 1, pp. 81–84 JANUARY, 1947

NOTEWORTHY PLANTS OF SOUTH AMERICA—IV. THREE VARGAS SPECIMENS[1]

PAUL C. STANDLEY AND FRED A. BARKLEY

Among a series of specimens studied which were collected by C. Vargas C., were four specimens representing three species apparently undescribed. Descriptions of these follow.

Cajophora Vargasii Standley & Barkley, sp. nov. Herbacea scandens; caulibus tortuosis, gracilibus; petiolis circa 20 mm. longis, setosis, pilosis; laminis deltoido-lanceolatis, supra sparse et subtus dense setuloso-pilosis, 35–95 mm. longis, 18–42 mm. ad basim latis, breviter, acuminatis, serrato-lobatis, lobis serratis; pedunculis gracilibus, tortuosis, circa 10 cm. longis, pilosis; sepalis 5, deltoido-lanceolatis, serratis, pilosis, circa 13 mm. longis, 5 mm. ad basim latis; petalis cymbiformibus, 30 mm. longis, 15 mm. latis, ad nervum villosulis, squamis saccatis, convexis, rotundo-ovatis, 5 mm. longis, 4 mm. latis, venis 3, appendicibus 3, filiformibus, circa 3 mm. longis, 0.7 mm. ad basim latis; staminodiis filiformibus ad circa 13 mm. longis, 1 mm. ad basim latis; staminibus circa 80; capsulis piloso-setosis.

Setulose vine with slender, brownish, tortuous stems; petioles about 20 mm. long, setose, pilose; leaf-blades deltoid-lanceolate, setulose-pilose above and densely so on under surface, 35–95 mm. long, 18–42 mm. broad near base, short acuminate, serrately lobed from base, lobes obscurely serrate; peduncles slender, tortuous, about 10 cm. long, appressed pilose; sepals 5, deltoid-lanceolate, serrate, pilose, about 13 mm. long, 5 mm. broad at base, petals cymbiform, 30 mm. long, 15 mm. wide, villosulous especially on the veins, whitish; scales yellowish, saccate, convex, rotund-ovate, 5 mm. long, 4 mm. wide, 3-nerved, bearing dorsally near the apex 3 filiform appendages about 3 mm. long and 0.7 mm. wide at their base, staminodia filiform to about 13 mm. long, 1 mm. broad at base; stamens about eighty; filaments slender, about 25 mm. long; anthers black, ovoid, about 1 mm. long; capsule twisted, pilose-setose.

PERU: "en un bosque de *Polylepis, Schinus, Eugenia,* etc.," 3600 meters, Departamento Cuzco, Provincia Paruro, 19 I 1942, *C. Vargas C. 2392* in Herb. Chic. Nat. Hist. (Field) Mus., TYPE.

A second specimen, *C. Vargus C. 2657* (from open forest, 2800 meters altitude, Tuncapata, Santa Rita, Dep't Cuzco, Prov. Urubamba, Peru, in Herb. Chic. Nat. Hist. (Field) Mus.) is apparently conspecific; it is almost identical in foliage, but the flower parts are about two-thirds as large. A third specimen, *Benj. Styles,* 18 Aug 1945 (in Herb. Chic. Nat. Hist. (Field) Mus.) apparently belongs here also.

This species is very similar to *Cajophora tenuis* Killip, but is at once distinguishable by the hispid capsule of that species. It is probably closest in relationship to *C. macrantha* Killip, but the leaves of that species are

[1] Publication is partly at the expense of Fred A. Barkley.

hispid, the lobes more sharply dentate, the lobing is much deeper, the flowers are larger, and the glands are without the dorsal appendages.

Sicyos Vargasii Standley & Barkley, sp. nov. Herbacea scandens, caule gracili striate sparse caduceque pilosus, internodiis elongatis; folia petiolata membranacea, orbicularia, albido-papillosa, petiolo crasso circa 5 cm. longo; lamina 6–9 cm. longa et subaequilata profunde quinquelobata; basi profunde cordata; inflorescentia pedunculata, floribus numerosis racemosis densis, pedicellis gracilibus ad 6 mm. longis; calyxibus 5-lobis; petalis 5; staminibus connatis, antheris contortis; fructibus immaturis fugaciter pilosis.

Sprawling, tendrilled, succulently herbaceous vine; stems soon glabrous, striate; tendrills 1- to 2-parted; petioles coarse, to about 5 cm. long, soon glabrous; leaf-blades 6–9 cm. long, thinly membranaceous, ovate in outline and 5-lobed with lobes acutish except the terminal lobe acuminate to (as is the commoner case) orbicular and twice lobate with lobe apex rounded-truncate to subacute, base cordate with a narrowly U-shaped sinus, short-white-papillose, puberulent on veins; peduncle of raceme to 10 cm. long, slender, fugaciously pilose, pistillate flowers clustered with staminate; perianth of pistillate flowers reduced; calyx of staminate flowers about 5 mm. broad, white, deeply 5-lobed; petals 5; filaments connate, anthers sessile, connate, flexuous; ovary ovoid, fugaciously pilose.

PERU: "Putac-llanco," annual vine among herbaceous plants on rocky slopes, near Asuncion Bridge, Rio Apurimac, Depto. Cuzco, Prov. Canas, Feb. 28, 1939, *C. Vargas 11025* in Herb. Chic. Nat. Hist. (Field) Mus., TYPE.

Loasa Raimondii[2] Standley & Barkley, sp. nov. Herba annua (vel perennans?); caulibus pilosis hispidulosisque, striatis, internodiis circa 7 cm. longis; foliis simplicibus, petiolatis; petiolis hispidulis, circa 1 cm. longis; laminis hispidulis pilosisque, 10–20 mm. latis, 45–30 mm. longis, irregulariter sinuato-dentatis, late lanceolatis, acutis, ad basim angustis inflorescentiis foliatis-racemosis; pedicellis circa 18 mm. longis; sepalis viridibus, ovatis, acutis, pilosis setosisque, circa 4 mm. longis; petalis planis, membranaceis, albis, obovatis, subacutis, circa 10 mm. longis; squamis inflatis, 2 mm. latis, 3 mm. longis; staminibus multis, fasciculatis, circa 6 mm. longis; capsulis circa 20 mm. longis, 5 mm. latis, hispidis pilosisque.

Subscandent or sprawling, coarse annual (or perennial?); stem yellowish, pilose, setose, striate, internodes about 7 cm. long; leaf simple, petiolate; petiole hispid and pilose, about 1 cm. long; blade sparsely setose and sparsely pilose, 10–20 mm. broad, 45–30 mm. long, irregularly sinuate-dentate, broadly lanceolate, acute, narrowed toward base, abruptly truncate at base, rarely ovate and 5-lobate; inflorescence a leafy subscorpioid raceme; flower large; pedicels not adnate to the axis, about 18 mm. long in fruit; sepals green, ovate, acute, pilose and setose, about 4 mm. long; petals white, obovate, subacute, about 10 mm. long, clawed, pilose and setose, spinose-ciliate; scales inflated, scarcely saccate at base, 2 mm. wide, 3 mm. long; stamens many, fasciculate and opposite the petals, about 6 mm. long; capsule about 20 mm. long, 5 mm. broad, subobconical, hispid and pilose, 3-valved, the valves alternating with the sepals; seeds many, rough, angular, about 1 mm. in diameter.

[2] Honoring Antonio Raimondi.

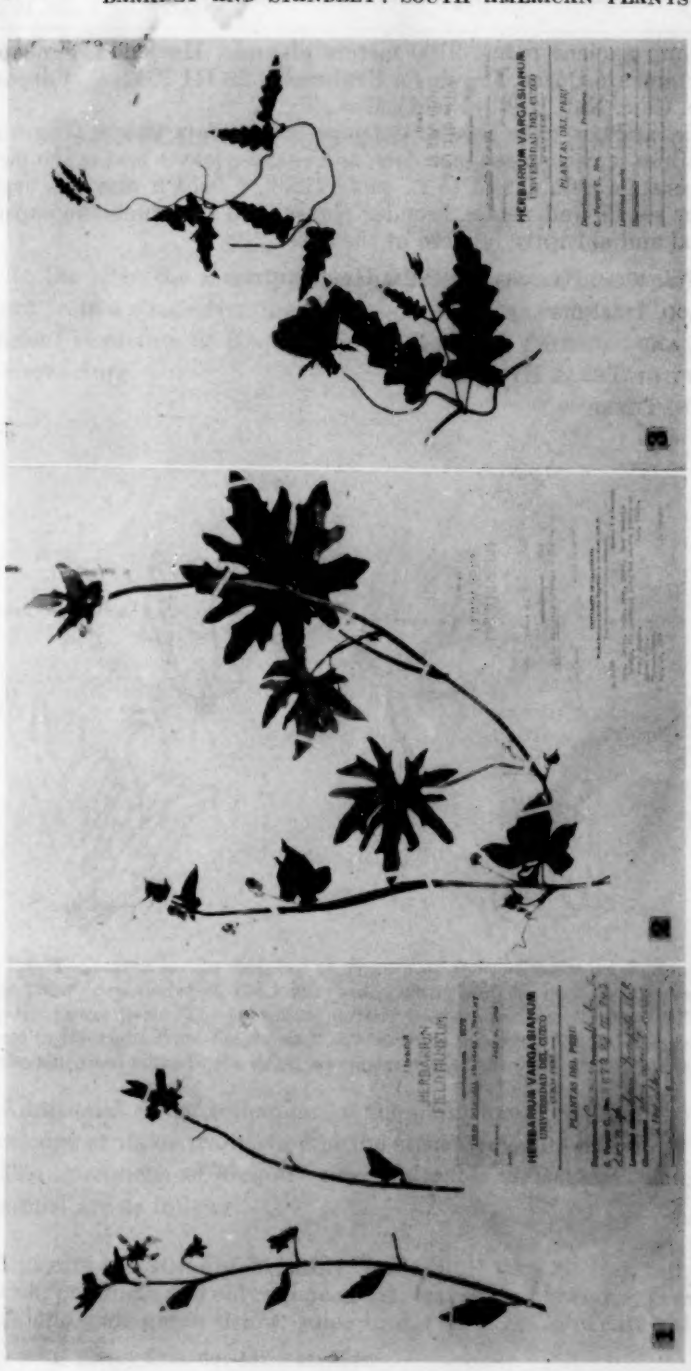


FIG. 1. Type sheet of *Loasa Raimondii* Standl. & Barkl., Departamento Cusco, Peru, 28 March 1942, *Vargas 2672* in Herb. Chic. Nat. Hist. (Field) Mus. 1164358. FIG. 2. Type sheet of *Sicyos Vargasii* Standl. & Barkl., Departamento Cusco, Peru, 28 February 1929, *Vargas 11025* in Herb. Chic. Nat. Hist. (Field) Mus. 1164359. FIG. 3. Type sheet of *Cajophora Vargasii* Standl. & Barkl., Departamento Cusco, Peru, 19 January 1942, *Vargas 2392* in Herb. Chic. Nat. Hist. (Field) Mus. 1164356.

PERU: Along ancient ruins, 2100 meters altitude, Hacienda Tuncapata Stihit, Departamento Cuzco, Provincia Urubamba, 28 III 1942, *C. Vargas C. 2672* in Herb. Chic. Nat. Hist. (Field) Mus., TYPE.

This species appears to be related to *Loasa carunculata* Urb. & Gilg which has densely pilose-setose, more lanceolate, and coarser leaves and much larger flowers with orange petals, and to *L. picta* Hook. f. which also has orange petals, shorter sepals and petals, broader leaves, and on which the capsules are cylindrical and abruptly tapered at the base.

CHICAGO NATURAL HISTORY MUSEUM HERBARIUM
CHICAGO, ILLINOIS
AND
UNIVERSITY OF TEXAS HERBARIUM
AUSTIN, TEXAS

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 1, PP. 85–86 JANUARY, 1947

NOTEWORTHY PLANTS OF SOUTH AMERICA—V. THE GENUS OCHOTERENAEA

FRED A. BARKLEY

At the time the monotypic genus *Ochoterenaea* was published[1] it was known from a single fruiting collection. From its compact thyrsus of fruits, sufficient remnants of flowers were available to furnish some knowledge of their structure.

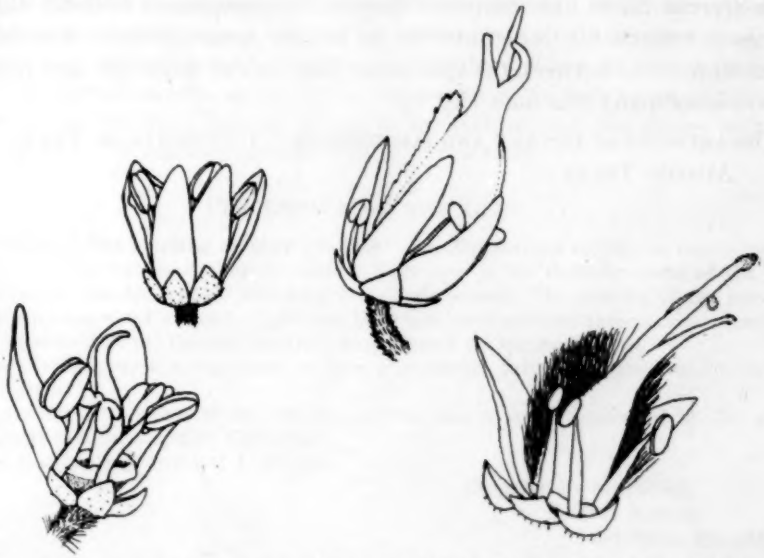


FIG. 1. Camera lucida sketches of flowers of *Ochoterenaea columbiana* Barkley. The upper from dried material, the lower boiled material with some petals removed to better show the flower parts. The staminate flowers to the left from *Garcia 10748*, the pistillate flowers to the right from *Steyermark 56745*. Note the mat of glandular substance obscuring the marginal hairs in the dried specimen of pistillate flower. Drawings × 12.

Additional recent collections of the plant have been made so that further knowledge of its distribution and the structure of its flowers is available.

The specimens of *Ochoterenaea columbiana* Barkley which have been examined are as follows.

VENEZUELA: state of Mérida: "cedrillo," tree 30 feet tall, flowers dull whitish, peduncle and calyx pale green, leaves membranous, grass-olive green above and pale green below, juice in cut stem milky, fruit pale green with

[1] Bull. Torrey Club 69: 442–444. 1942.

lavender silky margin, ovary fragrant-spicy, rich forested slopes along Río Onia, near Bolero, north of Mesa Bolívar, alt. 550–915 mtrs., 23 May 1944, *Julian A. Steyermark 56745* [Herb. Chicago N. H. (Field) Museum, Herb. U. Texas]. COLOMBIA: department El Valle: dense forest, Rio Digua Valley, between La Elsa and Rio Blanco, alt. 725 mtrs., 2–5 April 1939, *E. P. Killip 34772* (Herb. U. S. Nat., TYPE); department Cundinamarca: arbol mas menos 4 mtrs., La Vega, Camino a Nocaima, alt. 1200–950 mtrs., 27–29 Enero 1942, *H. Garcia Barriga 10640* (Herb. U. S. Nat.); entre Pacho y Rio Negro, carretera y alrededores, alt. 1000–1200 mtrs., 22–26 Febrero 1942, *H. Garcia Barriga 10748* (Herb. U. S. Nat.).

Killip 34772 has mature fruits, *Garcia 10640* has immature fruit, *Steyermark 56745* contains pistillate flowers, immature fruit, and mature fruit, while *Garcia 10748* has staminate flowers. The specimens indicate that the species is remarkably constant over its known range, as only minute variations were noted between the specimens. Sketches of staminate and pistillate flowers accompany this note (fig. 1).

DEPARTMENT OF BOTANY AND BACTERIOLOGY, UNIVERSITY OF TEXAS
AUSTIN, TEXAS

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 74, NO. 1, PP. 87–88 JANUARY, 1947

TORREYA

An Apparently New Record of Globulinea gigantea Ulke. Dr. Curt Teichert, of the University of West Australia, Crawley (Perth), Australia, has figured what appears to be *Globulinea gigantea* Ulke in figure 4 of an article in Bull. Am. Assoc. Petroleum Geologists **25**(3): 385. Mr 1940. This fossil alga has hitherto been found only in Indiana limestone. Dr. Teichert's specimen was found in the Kimberly District of northwestern Australia in ferruginous sandstone (Liveridge Series) of Upper (Permian) Paleozoic Age. He called it a "Large Gastropod Trail." This diagnosis seems inapplicable, however, for a marine gastropod trail would evidently show only on the surface and would hardly extend into sandstone rock, originally mud of course, as illustrated. These gastropod trails, or mud-eating *Nereites* tracks, appear to be five-eighths of an inch across judging by the size of the geologist's hammer shown in the picture, and this agrees with the size of the axis of *Globulinea gigantea* Ulke.—TITUS ULKE.

PROCEEDINGS OF THE CLUB

Minutes of the Meeting of May 15, 1946. Dr. Zimmerman called the regular meeting of the Torrey Botanical Club to order at 3:30 p.m. in the members room of the New York Botanical Garden with 18 members and guests present. The minutes of the previous meeting were approved as read. Eight new associate members and three annual members, already approved at the Council meeting, were elected by the members.

The Club approved a resolution to have a memorial written for the late Dr. Robert Almer Harper.

The scientific portion of the day's program was a paper presented by Dr. J. S. Karling on: "Keratinophilic Chytrids."

The meeting adjourned at 4:30 p.m.

Respectfully submitted,
LIBERO AJELLO
Recording Secretary

Minutes of the Meeting of October 1, 1946. Dr. Zimmerman opened the first fall meeting of the Torrey Botanical Club at 8:15 p.m. at the Brooklyn Botanic Garden. Twenty members and friends were present. The minutes of the previous meeting were approved as read.

Dr. Simpson was in receipt of a letter from Cuba requesting information on the relation of *Chara* to mosquito control. The letter was turned over to Dr. Johnson, who was to refer it to the Department of Entomology, Rutgers University.

No further business was transacted and the meeting was opened to an informal discussion of the summer activities of the members.

The meeting adjourned at 9:45 p.m., refreshments being served by the staff of the Brooklyn Botanic Garden.

Respectfully submitted,
LIBERO AJELLO
Recording Secretary

Report of the Committee to Prepare a Memorial for the late Dr. Robert Almer Harper. October 16, 1946. As an appropriate feature of the celebration of the Seventy-

fifth Anniversary of the Founding of The Torrey Botanical Club, Volume 69, 1942, of the BULLETIN was dedicated to Robert Almer Harper and Herbert McKenzie Denslow. The May number of that volume, containing a brief biographical sketch, was specifically designated as the "Harper Number." Today The Torrey Botanical Club again pays its respects, through this Memorial, to Professor Harper, who died at his home near Bedford, Virginia, May 12, 1946.

Robert Almer Harper was elected to membership in the Club October 10, 1911. From his boyhood days at Port Byron, Illinois, he had been greatly interested in the plants of the regions wherever he lived. On coming to New York he continued this interest especially in the local Cryptogamic Flora. It was only natural that soon after he became President of the Club January 13, 1914, he should ask permission to appoint a number of persons to be Chairmen of Special Committees on Local Flora. Accordingly he appointed twenty-four such chairmen, and he himself undertook to do special work on the genus *Cortinarius*. This list of Chairmen, with necessary changes, has been continued and published in TORREYA.

Professor Harper strongly supported the movement to establish a class of membership to include those to be known as Associate Members. He was one of the first to become a Sustaining Member and he maintained this membership until his death.

When we read the Proceedings of the Club and News and Notes published in TORREYA since 1911, we are made to realize how wide were his interests in the plant sciences and his many contributions to the welfare of the Club. By his death Botany lost a great investigator and teacher, the Club lost one of its most enthusiastic supporters, and his colleagues a good friend and counselor. Therefore,

Be it resolved that this memorandum be recorded in the minutes of this meeting and published with the Proceedings of the Club. It is also directed that copies of these minutes be transmitted to Mrs. Harper and other members of the family with expressions of the deepest sympathies of the members of the Club.

(Signd) B. O. DODGE
JOHN S. KARLING
H. W. RICKETT

NEWS NOTE

The following appeal was sent to the President of the Club through the Office of Foreign Relations, Manila:

"At the outbreak of World War II, the Scientific Library of the Bureau of Science, an office under this Department, had one of the largest and best known collections of technical and scientific publications in this part of the Orient. This same library was destroyed by the Japanese during the war.

"We shall appreciate it, therefore, if you will kindly help us in the task of building anew from scratch some such collection by donating to the library whatever publications you can spare now and in the future. Please send them addressed to: Scientific Library, Bureau of Science, Manila, Philippines."

(Signed) JOSE S. CANUS
Under Secretary

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY
LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used to include the entire Western Hemisphere.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the Bibliographer to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. The different subjects as classified below may be ordered separately (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Club.

TAXONOMY, PHYLOGENY AND FLORISTICS

ALGAE

(See also under Morphology: **Hall**; under Physiology: **Smith.**)

Allen, W. E. "Red water" in La Jolla Bay in 1945. Trans. Am. Micros. Soc. **65:** 149–153. Ap 1946.

Jahn, Theodore Louis. The euglenoid flagellates. Quart. Rev. Biol. **21:** 246–274. *6 f.* S [O] 1946.

Sampaio, Joaquim. Desmidias portuguesas. Bol. Soc. Broteriana **18:** 5–559. *pl. 1–17.* 1944. [The plates occupy p. 479–517. pp. 539–550 are unnumbered.]

Tiffany, Lewis Hanford. The Oedogoniaceae. II. Bot. Rev. **12:** 530–534. N 1946.

FUNGI AND LICHENS

(See also Phytopathology; and under Morphology: **Carvajal, Nagel.**)

Ahmad, Sultan. The genus *Poronia* in India. Lloydia **9:** 139–143. Je [S] 1946.

Barnet, Horace L. New reports of Iowa fungi. Proc. Iowa Acad. **52:** 95–100. 1945 [Jl 1946].

Bier, J. E. & Nobles, Mildred K. Brown pocket rot of Sitka spruce. Canad. Jour. Res. C **24:** 115–120. *f. 1–12.* Au 1946.

Bitancourt, A. A. Novas especies sul-americanas do genero *Elsinoë.* Arq. Inst. Biol. [São Paulo] **16:** 19–26. *pl. 4–7.* 15 N 1945.

Carvajal, Fernando. Biologic strains of *Streptomyces griseus.* Mycologia **38:** 596–607. *f. 1–4.* S–O 1946.

Doty, Maxwell Stanford. *Clavaria,* the species known from Oregon and the Pacific Northwest. Oregon State Monog. Stud. Bot. **7:** 1–91. *illust.* D 1944.

Drechsler, Charles. Several species of *Pythium* peculiar in the sexual development. Phytopathology **36:** 781–864. *f. 1–29.* O 1946.

Gilman, Joseph C. Illustrations of the fleshy fungi of Iowa. VII. Some common puff balls. Proc. Iowa Acad. **52:** 113–119. *f. 1–6.* 1945 [Jl 1946].

Herre, Albert W. The lichen flora of the Philippines. Jour. Arnold Arb. **27:** 408–412. 15 O 1946.

Latham, R. Additional notes on *Cetraria islandica* (L.) Ach. on Long Island. Bryologist **49:** 71. Je 1946.

Lindquist, Juan C. *Ravenelia Hassleri* Speg. igual a *Ravenelia Dieteliana* P. Henn. Bol. Soc. Argent. Bot. **1**: 123–125. *1 f.* Ap 1946.

Ling, Lee & Tai, M. C. New Peronosporaceae from China. Lloydia **9**: 144, 145. *f. 1–4.* Jl [S] 1946.

Lombard, Frances F. & Davidson, Ross. W. An undescribed *Coryneum* on diseased Italian cypress. Phytopathology **36**: 775–777. *f. 1.* S 1946.

Long, W. H. The genus *Phellorina.* Lloydia **9**: 132–138. *f. 1–9.* Je [S] 1946.

Luttrell, E. S. The genus *Stomiopeltis* (Hemisphaeriaceae). Mycologia **38**: 565–586. *f. 1–20.* S–O 1946.

Meehan, Frances & Murphy, H. C. A new *Helminthosporium* blight of oats. Science **104**: 413, 414. 1 N 1946.

Miller, J. J. Cultural and taxonomic studies on certain *Fusaria.* I. Mutation in culture. Canad. Jour. Res. C. **24**: 188–212. *pl. 1,2.* O 1946; II. The taxonomic problem in *Fusarium* with particular reference to section *elegans.* 213–223.

Newhall, A. C. More on the name *Ansatospora acerina.* Phytopathology **36**: 893–896. O 1946.

Olive, Lindsay S. Some taxonomic notes on the higher fungi. Mycologia **38**: 534–547. *f. 1–4.* S–O 1946.

Savile, D. B. O. *Entyloma fuscum* and related smuts attacking Papaveraceae. Canad. Jour. Res. C. **24**: 109–114. *f. 1–5.* Au 1946.

Seaver, Fred J. Photographs and descriptions of cup-fungi. XLII. *Gorgoniceps.* Mycologia **38**: 548–553. *f. 1, 2.* S–O 1946.

Singer, Rolf. Type studies on agarics—II. Lloydia **9**: 114–131. Je [S] 1946.

Singer, Rolf & Smith, Alexander H. The taxonomic position of *Pholiota mutabilis* and related species. Mycologia **38**: 500–523. *f. 1–10.* S–O 1946.

Stevenson, John A. Fungi novi denominati—II. Mycologia **38**: 524–533. S–O 1946.

Viégas, A. P. & Teixeira, Cyro G. Alguns fungoa de Minas Gerais. Rodriguésia 9^{19}: 49–56. *pl. 1–6.* S–D 1945.

BRYOPHYTES

Brown, Margaret S. Bryophytes of Nova Scotia: Addition to July, 1945. Bryologist **49**: 102, 103. S 1946.

Flowers, S. *Encalypta ciliata* var. *pilifera* n. var. Bryologist **49**: 84. Je 1946.

Frye, T. C. & Clark, L. Attu Island bryophytes collected by Hardy. Bryologist **49**: 59–65. Je 1945.

Gates, F. C. Moss in the revegetation of an area in northern Michigan. Bryologist **49**: 66–71. Je 1946.

Grout, Abel Joel. Bryales: Orthotrichaceae. N. Am. Flora **15 A**^{1}: 1–62. *pl. 1–5.* 4 N 1946.

Haring, Inez M. Mosses of the Grand Canyon National Park, Arizona, II. Bryologist **49**: 90–96. *2 f.* S 1946.

Persson, H. Some Alaskan and Yukon bryophytes. Bryologist **49**: 41–58. Je 1946.

Richards, P. W. *Pseudohypnella guianensis* a synonym of *Hypnella cymbifolia.* Bryologist **49**: 88. Je 1946.

Saintsbury, G. O. K. *Dicranodontium australe* Dixon. Bryologist **49**: 100–102. S 1946.

Sharp, Aaron J. Bryological notes from Mexico, III. Bryologist **49**: 89. S 1946.

Steere, W. C. Mosses of British Honduras and the Department of Peten, Guatemala. III. Bryologist **49**: 72–84. Je 1946.

Wareham, R. T. A new moss species *Atrichum paraphyllium*. Bryologist **49**: 85, 86. Je 1946.

PTERIDOPHYTES

Clausen, Robert T. *Selaginella*, subgenus *Euselaginella*, in the southeastern United States. Am. Fern. Jour. **36**: 65–82. *pl. 2–6 + f. 1–5*. J–S [O] 1946.

Copeland, Edwin B. Parallel and convergent evolution in ferns. Jour. Arnold Arb. **27**: 355–360. 15 O 1946.

Fernald, M. L. The presumable identity of *Cheilanthes lanosa*. Rhodora **46**: 383–388. N 1946.

Fernald, M. L. Some trivial American forms of the lady-fern. Rhodora **48**: 389–391. N 1946.

Frick, T. A. Some ferns of Claiborne County, Tennessee. Jour. Tenn. Acad. **21**: 266, 267. Jl 1946.

Maxon, William R. New Cyatheaceae from Colombia. Jour. Arnold Arb. **27**: 438–441. *pl. 1*. 15 O 1946.

Maxon, William R. & Morton, C. V. Two new ferns from Colombia. Am. Fern Jour. **36**: 91–94. Jl–S [O] 1946.

Moore, J. W. & Tryon, R. M. A new record for *Isoetes melanopoda*. Am. Fern Jour. **36**: 89–91. Jl–S [O] 1946.

Weatherby, C. A. "Notholaena" in Brazil. Jour. Arnold Arb. **27**: 361–370. *pl. 1, 2*. 15 O 1946.

Weatherby, C. A. A variety of *Athyrium decurtatum* from Argentina. Am. Fern Jour. **36**: 94, 95. Jl–S [O] 1946.

Woodson, Robert E. Memorabilia filicum panamensium. Am. Fern Jour. **36**: 82–89. *pl. 7*. Jl–S [O] 1946.

SPERMATOPHYTES

Abercrombie, R. G. Variation of the broadleaved helleborine [*Epipactis latifolia*] in the Peak district. Northwest Nat. **20**: 226–228. S–D 1945.

Anderson, W. A. *Verbascum phlomoides* near Iowa City. Proc. Iowa Acad. **52**: 91, 92. 1945. [Jl 1946,]

[**Anon.**] Expansion of plant systematics. Nature **158**: 535, 536. 1946.

Apolinar María, *Hermano*. Vocabulario de términos vulgares en historia natural colombiana (Continuación). Revista Acad. Colomb. **6**: 467–483. 1946.

Ball, Carleton R. More plant study: fewer plant names [in *Salix*]. Jour. Arnold Arb. **27**: 371–385. 15 O 1946.

Beetle, Alan A. Studies in the genus *Scirpus* L. VIII. Notes on its taxonomy, phylogeny, and distribution. Am. Jour. Bot. **33**: 660–666. O [N] 1946.

Borsini, O. E. Valerianaceae. *In:* Descole, Genera et species plantarum argentinarum **2**[1]: 275–372. *pl. 122–170*. 6 N 1944.

Brade, A. C. Contribuição para o conhecimento da flora dos parques nacionais de Itatiaia e Serra dos Órgãos. I. Labiatae. Rodriguésia **9**[19]: 9–20. *pl. 1–10*. S–D 1945.

Brenckle, J. F. Notes on the *Avicularia*. II. Phytologia **2**: 169–171. 20 S 1946.

Burkill, I. H. On the dispersal of the plants most intimate to Buddhism. Jour. Arnold Arb. **27**: 327–339. 15 O 1946.

Cardenas, M. Notas cactológicas sobre el genero *Lobivia* de Bolivia. Revista Agr. [Cochabamba] **2**: 85–87. Je 1945.

Castellanos, A. *In:* Descole, Genera et species plantarum argentinarum 3: 1–382 [Farinosae 1–4, Centrolepidaceae 5–19, *pl. 1, 2.* 15 Mr 1945; Mayaceae 21–37, *pl. 3–5.* 20 Je 1945; Xyridaceae 39–66, *pl. 6–13.* 9 Jl 1945; Eriocaulaceae 67–104, *pl. 14–21.* 30 Au 1945; Bromeliaceae 105–382. *pl. 22–133.* 23 S 1945.] Buenos Aires 1945.

Chevalier, Aug. Révision du genre *Theobroma,* d'après l'Herbier du Muséum national d'Histoire naturelle de Paris. Revue Bot. Appl. Agr. Trop. **26:** 265–285. *2 pl.* Jl–Au 1946.

Clausen, R. T. A new sub-species of *Sedum ebracteatum* [*grandifolium*] from the Sierra Madre del Sur [Mexico]. Cactus & Succ. Jour. **18:** 86, 87. Je 1946.

Coker, William Chambers & Totten, Henry Roland. Trees of the southeastern states including Virginia, North Carolina, South Carolina, Tennessee, Georgia, and northern Florida. 3rd ed. *i–vii,* 1–419. *illust.* Univ. No. Carolina Press, 1945.

Corner, E. J. H. Centrifugal stamens [and phylogeny]. Jour. Aronld Arb. **27:** 423–437. *f. 1–7.* 15 O 1946.

Cory, V. L. A white *Gaillardia* in Texas. Madroño **8:** 263, 264. O [5 N] 1946.

Cuatrecasas, Jose. Notas a la flora de Colombia, VIII. [Araliaceae, etc.]. Revista Acad. Colomb. **6:** 533–551. *f. 1–4 + pl. 1–4.* 1946.

Cutler, Hugh C. Races of maize in South America. Bot. Mus. Leafl. **12:** 257–291. *pl. 34–37 + f. 1–4.* 25 O 1946.

Dugand, Armando. Nuevas nociones sobre el género *Ficus* en Colombia, V. Caldasia **4:** 113–120. 15 Au 1946.

Eaton, Richard J. *Dicentra eximia* in Vermont. Rhodora **48:** 272, 273. 19 O 1946.

Fabregat, Julio T. Nuevas cactáceas uruguayas. Revista Acad. Colomb. **6:** 571, 572. 1946.

Fernald, M. L. Does *Bartonia verna* grow in Virginia? Rhodora **48:** 327, 328. 19 O 1946.

Fernald, M. L. *Senecio tomentosus,* forma *alabamensis.* Rhodora **48:** 330, 331. N 1946.

Fernald, M. L. Types of some American trees. Jour. Arnold Arb. **27:** 386–394. *pl. 1–3.* 15 O 1946.

Foxworthy, F. W. Distribution of the Dipterocarpaceae. Jour. Aronld Arb. **27:** 347–354. 15 O 1946.

Frick, T. A. Some problems with reference to *Chelone glabra* var. *elator.* Jour. Tenn. Acad. **21:** 283, 284. Jl 1946.

Hill, H. South American Cacti. VIII. Desert **18:** 85, 86. Je 1946.

Hoehne, F. C. Novidades para as Orchidaceas de S. Paulo e Paraná. Arq. Bot. Estado São Paulo **2:** 21–27. *pl. 8–11.* Mr 1946.

Holttum, R. E. The classification of Malayan bamboos. Jour. Arnold Arb. **27:** 340–346. 15 O 1946.

Hull, Edwin D. *Centaurea maculosa* in Indiana. Rhodora **48:** 391. N 1946.

Humbert, Henri. La protection de la nature à Madagascar. Jour. Arnold Arb. **27:** 470–479. *pl. 1–5 + f. 1.* 15 O 1946.

Jaques, H. E. & Hilleary, Doris. A thirty year's phenological record of the spring flowering plants of Henry County [Iowa]. Proc. Iowa Acad. **52:** 149–152. *f. 1.* 1945 [Jl 1946].

Kelso, Leon. The Rocky Mountain flora. I. The willows. Biol. Leafl. **34:** 1–11. 4 O 1946.

Kilbourne, Frederick W. Second station for *Corydalis flavula* in Connecticut. Rhodora **48**: 326, 327. 19 O 1946.

Leite, J. Eugenio. Duas novas espécies de orchidaceas de flora de Campos do Jardão. Arq. Bot. Estado São Paulo II. **2**: 19, 20. *pl. 6–9.* Mr 1946.

[**Little, Elbert L.**] Check list of native and naturalized trees of the United States, including Alaska. U.S.D.A. Forest Service 1–325. 15 Ap 1944. [Mimeographed—provisional.]

McAtee, W. L. Some local names of plants—IX. 1–16. privately printed. O 1946.

McClintock, Elizabeth & Epling, Carl. A revision of *Teucrium* in the New World, with observations on its variation, geographical distribution and history. Brittonia **5**: 491–510. 6 S 1946.

MacDougall, T. M. Field notes on some epiphytic cacti in the Chontal Region of Oaxaca, Mexico. Cactus & Succ. Jour. **18**: 147–150. *f. 93–101.* O 1946.

Maguire, Bassett. Studies in the Caryophyllaceae. II. *Arenaria Nuttallii* and *Arenaria filiorum*, section *Alsine*. Madroño **8**: 258–263. O [5 N] 1946.

Merrill, E. D. Le genre *Cleistocalyx* Blume (Myrtacées) serait-il à préférer au genre *Acicalyptus* A. Gray? Bull. Soc. Bot. France **86**: 377–379. 1940.

Meyer, T. Asclepiadaceae. *In:* Descole, Genera et species plantarum argentinearum **2**[1]: 1–273. *pl. 1–121.* 9 O 1944.

Miller, Robert C. *Linaria minor* (L.) Desf. in Johnston County, Iowa. Proc. Iowa Acad. **52**: 153. 1945 [Jl 1946].

Moldenke, H. N. Additional notes on the genus *Amasonia*. I. Phytologia **2**: 198–200. O 1946.

Moldenke, H. N. Additional notes on the genus *Petrea*. I. Phytologia **2**: 171–184. 20 S 1946; II. 195–198. O. 1946.

Monachino, Joseph. A revision of *Dyera* (Apocynaceae). Lloydia **9**: 174–202. S 1946.

Moyle, J. B., Nielsen, E. L. & Younge, O. R. Vegetation of artificial lakes in northwestern Arkansas. Rhodora **48**: 329, 330. N 1946.

Muenscher, Walter C. The vegetation of Bergen Swamp [Gennessee County, N. Y.]. I. The vascular plants. Proc. Rochester Acad. **9**: 64–117. *1 map.* Je 1946.

Munz, Philip A. *Fuchsia colombiana*, new species. Caldasia **4**: 109–111. *1 f.* 15 Au 1946.

Occhioni, Paulo. Contribuição para o conhecimento da flora do Distrito Federal (nota prévia). Rodriguésia **9**[19]: 57–65. S–D 1945.

Palmer, Ernest J. *Crataegus* in the northeastern and central United States and adjacent Canada. Brittonia **5**: 471–490. 6 S 1946.

Parodi, Lorenzo R. *Agrostis Ramboi*, nueva especie de Graminea del Brasil perteneciente a una nueva sección del género. Bol. Soc. Argent. Bot. **1**: 119–122. *1 f.* Ap 1946.

Ponce de Leon, Antonio. Joyas de la flora cubana. La ceiba (*Ceiba pentandra* Gaertn.). Revista Soc. Cub. Bot. **3**: 31. *illust.* Mr–Ap 1946.

Quisumbing, Eduardo. A critical study of Philippine species of the tribe Aquilarieae, family Thymelaeaceae. Jour. Arnold Arb. **27**: 401–407. 15 O 1946.

Rice, Mabel Agnes. Trees and shrubs of Nantucket; descriptions, identification keys, list of trees and shrubs. 1–77. *1 pl.* Marie Mitchell Assoc., Nantucket, Mass. 1946. [Lithoprinted.]

Schweinfurth, Charles. An addition to South American *Telipogon*. Am. Orchid Soc. Bull. **15**: 180–182. *1 pl.* 1 S 1946.

Schweinfurth, Charles. A fascinating new orchid from Cuba [in *Pleurothallis*]. Am. Orchid Soc. Bull. **15**: 234–236. *1 pl.* 14 O 1946.

Schweinfurth, Charles. Orchidaceae andinae—II. Revista Acad. Columb. **6**: 573–577. *pl. 1–7 + f. 1–9.* 1946.

Skottsberg, C. Observations of some shrubby Adesmiae of central Chile. Jour. Arnold Arb. **27**: 413–422. *f. 1, 2.* 15 O 1946.

Soukup, S. S. La Flora del Departamento de Puno [Peru]. [pars.] Bol. Soc. Geog. Lima **60**: 215–231. 1943.

Standley, Paul C. & Steyermark, Julian A. Flora of Guatemala Part 5. Fieldiana: Bot. **24**^{5}: 1–502. 27 Au 1946.

Stearn, William. Nomenclature and synonymy of *Allium odorum* and *A. tuberosum*. Herbertia **11** (1944): 227–245. *pl. 263 + f. 122.* 1946.

Steenis, C. G. J. van. Preliminary revision of the genus *Lonicera* in Malaysia. Jour. Arnold Arb. **27**: 442–452. *f. 1, 2.* 15 O 1946.

Stehlé, H. La nomenclature des végétaux économiques intéressant l'agriculture tropicale. Revue Bot. Appl. Agric. Trop. **26**: 256–264. Jl–Au 1946.

Toledo, J. F. Observações criticas sôbre nomes de algumas plantas brasileiras. Arq. Bot. Estado São Paulo II. **2**: 28–31. Mr 1946.

Toledo, J. F. *Pilea* ac *Smilaces* novae descriptae atque iconibus illustratae. Arq. Bot. Estado São Paulo II. **2**: 25–27. *pl. 12–14.* Mr 1946.

Uphof, J. C. T. Little known Allieae of southwestern North America. Herbertia **11** (1944): 246–253. 1946.

Van Melle, P. J. The junipers commonly included in *Juniperus chinensis*. Phytologia **2**: 185–195. O 1946.

Vélez, Ismael. Wild pineapples in Venezuela. Science **104**: 427, 428. 1 N 1946.

Weimarck, H. Studies in Juncaceae. With special reference to the species in Ethiopia and the Cape. Svensk Bot. Tids. **40**: 141–178. *14 maps.* [incl. distrib. in New World]. 28 Je 1946.

Wherry, Edgar T. A key to the cultivated Hostas. Nat. Hort. Mag. **25**: 253–256. *3 f.* Jl 1946.

Wiggins, Ira L. The type locality and type specimen of *Myrtillocactus cochal* (Orcutt) Britton and Rose. Cactus & Succ. Jour. **18**: 138, 139. S 1946.

Wood, Carroll E. *Setaria Faberii* in North Carolina. Rhodora **48**: 391, 392. N 1946.

PALEOBOTANY

Andrews, Henry N. & Lenz, Lee W. The Gallatin fossil forest. Ann. Mo. Bot. Gard. **33**: 309–313. *illust.* S 1946.

Brown, Roland W. [Taxonomic] Alterations in some fossil and living floras. Jour. Wash. Acad. **36**: 344–355. *f. 1–15.* 15 O 1946.

Hansen, Henry P. Postglacial forest succession and climate in the Oregon Cascades. Am. Jour. Sci. **244**: 710–734. *f. 1–4.* O 1946.

Kern, Ellen M. & Andrews, Henry N. Contributions to our knowledge of American carboniferous floras. IX. Some petrified seeds from Iowa. Ann. Mo. Bot. Gard. **33**: 291–306. *pl. 18, 19 + f. 1–5.* S 1946.

Reed, Fredda D. On *Cardiocarpon* and some associated plant fragments from Iowa coal fields. Bot. Gaz. **108**: 51–64. *f. 1–29.* 22 O 1946.

ECOLOGY AND PLANT GEOGRAPHY

(See also under Paleobotany: **Hansen**; under Bryophytes: **Gates.**)

Allard, H. A. Shale barren associations on Massanutten Mountain, Virginia. Castanea **11**: 71–124. *f. 1–10.* S [O] 1946.

Browne, George R. Vanishing original prairie area in Cedar Rapids, Iowa. Proc. Iowa Acad. **52**: 101–106. *f. 1.* 1945 [Jl 1946].

Daubenmire, R. F. The life zone problem in the northern intermountain region. Northwest Sci. **20**: 28–38. *1 f.* My 1946.

Hayden, Ada. The selection of prairie areas in Iowa which should be preserved. Proc. Iowa Acad. **52**: 127–148. *f. 1–7.* 1945 [Jl 1946].

Mason, Herbert L. The edaphic factor in narrow endemism. III. The geographic occurrence of plants of highly restricted patterns of distribution. Madroño **8**: 241–257. *f. 1.* O [5 N] 1946.

Ragonese, Arturo E. & Castiglioni, Julio A. Los pinares de *Aracucaria angustifolia* en la Republica Argentina. Bol. Soc. Argent. Bot. **1**: 126–127. *1 pl. + 1 map.* Ap 1946.

Rawitscher, Felix K. Algunas noções sôbre a vegetação do litoral brasileiro. Bol. Geog. Brasil **4**[8]: 13–28. *f. 1–9.* N 1944.

Rawitscher, Felix; Ferri, Mario G. & Rachid, Mercedes. Profundudade dos solos e vegetação em campos cerrados do Brasil meridional. Ann. Acad. Brasil. Cien. **15**: 267–294. *f. 1–8 + pl. 1, 2 + tables 1–7.* 31 D 1943.

Warner, Robert M. Vegetation and agriculture of Liberia and adjacent West Africa. Proc. Iowa Acad. **52**: 171–189. *f. 1–9.* 1945 [Jl 1946].

PHYTOPATHOLOGY

(See also Fungi)

Adsuar, José. Studies on virus diseases of papaya (*Carica papaya*) in Puerto Rico. I. Transmission of papaya mosaic. Univ. Puerto Rico Agr. Exp. Sta. Tech. Pap. **1**: 1–10. *f. 1–5.* Je 1946; II. Transmission of papaya mosaic by the green citrus aphid (*Aphis spiraecola* Patch.) **2**: 1–5. *1 f.* Je 1946.

Albert, W. B. The effects of certain nutrient treatments upon the resistance of cotton to *Fusarium vasinfectum*. Phytopathology **36**: 703–716. *f. 1–6 + tables 1–4.* S 1946.

Ark, Peter A. & Barrett, J. T. A new bacterial leaf spot of greenhouse-grown gardenias. Phytopathology **36**: 865–868. *f. 1.* O 1946.

Ark, Peter A. & Thomas, H. Earl. Bacterial leaf spot and bud rot of orchids caused by *Phytomonas cattleyae*. Phytopathology **36**: 695–698. *f. 1.* S 1946.

Ark, Peter A. & Tompkins, C. M. Bacterial leaf blight of bird's-nest fern. Phytopathology **36**: 758–761. *f. 1.* S 1946.

Ark, Peter A. & Tompkins, C. M. Leaf-nematode infestation of bird's-nest fern. Phytopathology **36**: 892, 893. *f. 1.* O 1946.

Berg, Anthony & Clulo, G. Genevieve. The relation of manganese to internal bark necrosis of apple. Science **104**: 265, 266. 20 S 1946.

Bohn, G. W. & Maloit, J. C. Bacterial spot of native golden currant (*Ribes aureum*). Jour. Agr. Res. **73**: 281–290. *f. 1–3.* 15 O 1946.

Buckland, D. C. Investigations of decay in western red cedar in British Columbia. Canad. Jour. Res. C. **24**: 158–181. *pl. 1–5 + f. 1–4.* O 1946.

Cochran, L. C. Passage of the ring spot virus through Mazzard cherry seeds. Science **104**: 269, 270. 20 S 1946.

Foister, C. E. The relation of weather to fungus diseases of plants. II. Bot. Rev. **12**: 548–591. N 1946.

Foster, R. E. The first symptom of tomato *Fusarium* wilt: clearing of the ultimate veinlets in the leaf. Phytopathology **36**: 691–694. *f. 1.* S 1946.

Heiberg, Barbara C. & Ramsey, Glen B. Fungistatic action of diphenyl on some fruit and vegetable pathogens. Phytopathology **36:** 887–891. O 1946.

Jenkins, John Mitchell. Studies on the inheritance of downy mildew resistance and of other characters in cucumbers. Jour. Hered. **37:** 267–271. *f. 6, 7.* S [O] 1946.

Joffily, J. M. Bacteriose da folhas da mamoneira [*Ricinus communis* L.]. Rodriguésia **9**[19]: 21–24. *pl. 1, 2.* S–D 1945.

Joffily, J. M. Cercosporiose da piteira [*Fourcroya gigantea* Vent.]. Rodriguésia **9**[19]: 25–28. *pl. 1–4.* S–D 1945.

Kienholz, J. R. & Childs, Leroy. Reduction in yield of the Anjou pear caused by wettable-sulphur spray. Phytopathology **36:** 777–779. *1 table.* S 1946.

Loucks, K. W. & Hopkins, E. F. A study of the occurrence of *Phomopsis* and of *Diplodia* rots in Florida oranges under various conditions and treatments. Phytopathology **36:** 750–757. *f. 1–7.* S 1946.

Menzies, J. D. Witches' broom of alfalfa in North America. Phytopathology **36:** 762–774. *f. 1, 2 + tables 1–3.* S 1946.

Pady, Stuart M. The development and germination of the intraepidermal teliospores of *Melampsorella Cerastii.* Mycologia **38:** 477–499. *f. 1–30.* S–O 1946.

Person, L. H. The soil rot of sweet potatoes and its control with sulphur. Phytopathology **36:** 869–875. *tables 1–5.* O 1946.

Pickett, B. S., *et al.* A disease of corn in the Rio Grande Valley of Texas. Iowa State Coll. Jour. Sci. **20:** 423–428. *f. 1, 2.* Jl 1946.

Quanjer, H. M. "Premunity" [vs. "acquired immunity"]. Phytopathology **36:** 892. O 1946.

Roberts, John W. Recent developments in fungicides. II. Spray materials—1936–1944. Bot. Rev. **12:** 538–547. N 1946.

Rudolph, B. A. Attempts to control bacterial blights of pear and walnut with penicillin. Phytopathology **36:** 717–725. S 1946.

Silberschmidt, K. Observações suplementares sôbre a transmissão experimental da "Clorose Infecciosa" das Malvaceas. Arq. Inst. Biol. [São Paulo] **16:** 49–64. *pl. 9–12.* 15 N 1945.

Stakman, E. C. Plant pathologists' merry-go-round. A survey of the never-ending battle against plant diseases. Jour. Hered. **37:** 259–265. *f. 1–5.* S [O] 1946.

MORPHOLOGY

(including anatomy & cytology in part)

(See also under Genetics: **Lowe & Nelson.**)

Accorsi, Walter Radamés. Curiosa anomalia nas fôlhas de *Morus alba* L. Rodriguésia **9**[19]: 29–44. *f. 1–16.* S–D 1945.

Allard, H. A. Clockwise and counter-clockwise spirality in the phyllotaxy of tobacco. Jour. Agr. Res. **73:** 237–242. *f. 1 + table 1–3.* 15 S 1946.

Allen, George S. Embryology and development of the apical meristems of *Pseudotsuga.* I. Fertilization and early embryogeny. Am. Jour. Bot. **33:** 666–677. *f. 1–24.* O [N] 1946.

Artschwager, Ernst. Contribution to the morphology and anatomy of Cryptostegia (*Cryptostegia grandiflora*). U.S.D.A. Tech. Bull. **915:** 1–40. *f. 1–25.* Jl 1946.

Carvajal, Fernando. Studies on the structure of *Streptomyces griseus.* Mycologia **38:** 587–595. *f. 1–3.* S–O 1946.

Hall, P. Cytoplasmic inclusions of the plant-like flagellates. Bot. Rev. **12**: 515–520. N 1946.

Harling, Gunnar. Studien über den Blütenbau und die Embryologie der Familie Cyclanthacea. Svensk Bot. Tids. **40**: 257–272. *f. 1–4*. 26 S 1946.

Leach, J. G. & Ryan, Mary Alice. The cytology of *Ustilago striiformis* and *poae-pratensis* in artificial culture. Phytopathology **36**: 875–886. *f. 1–6*. O 1946.

Milanez, R. F. Anatomia das principais madeiras brasileiras das "Rutaceae." Rodriguésia **9**[10]: 45–47. *1 pl.* S–D 1945.

Murphy, John B. Megasporogenesis and development of the embryo sac of *Allium cernuum*. Bot. Gaz. **108**: 129–136. *f. 1–14*. 22 O 1946.

Mustard, Margaret J. & Lynch, S. J. Flower-bud formation and development in *Mangifera indica*. Bot. Gaz. **108**: 136–140. *f. 1–6*. 22 O 1946.

Nagel, Lillian. A cytological study of yeast (*Saccharomyces cerevisiae*). Ann. Mo. Bot. Gard. **33**: 249–288. *pl. 10–17*. S 1946.

Newcomer, Earl H. Concerning the duality of the mitochondria and the validity of the osmiophilic platelets in plants. Am. Jour. Bot. **33**: 684–697. *f. 1–41*. O [N] 1946.

Nielsen, Etlar L. The origin of multiple macrogametophytes in *Poa pratensis*. Bot. Gaz. **108**: 41–50. *f. 1–18*. 22 O 1946.

Prat, Henri. Les gradients histo-physiologiques et l'organogenèse végétale. Contr. Inst. Bot. Univ. Montréal **58**: 1–151. *f. 1–20*. 1945. [Rev. Canad. Biol. **4**: 543–693. 1945.]

Retke, R. V. The anatomy of circumscissile dehiscence. Am. Jour. Bot. **33**: 677–683. *f. 1–20*. O [N] 1946.

Richey, Frederick D. Corn cob fur. Jour. Hered. **37**: 250–252. *f. 16, 17*. Au [O] 1946.

Saksena, R. K. & Bhargava, K. S. Some cytological observations on spore formation in *Thraustotheca clavata*. Mycologia **38**: 554–564. *f. 1, 2*. S–O 1946.

Stout, A. B. The synflorescence of *Amaryllis* hybrids. Herbertia **11** (1944): 268–273. *pl. 268, 269*. 1946.

Traub, Hamilton P. Rickett's "The Classification of Inflorescences." Herbertia **11** (1944): 266, 267. 1946.

GENETICS

(including cytogenetics)

Arnason, T. J., Harrington, J. B. & Friesen, H. A. Inheritance of variegation in barley. Canad. Jour. Res. C. **24**: 145–157. *pl. 1*. O 1946.

Einset, John, Blaser, H. Weston & Imhofe, Barbara. A chromosomal chimera of the Northern Spy apple. Jour. Hered. **37**: 265, 266. S [O] 1946.

Goodspeed, T. H. Meiotic prophase phenomena in species and interspecific hybrids of *Nicotiana*. Jour. Arnold Arb. **27**: 453–469. *pl. 1–3 + f. 1*. 15 O 1946.

Huskins, C. Leonard. Fatuoid, speltoid and related mutations of oats and wheat. Bot. Rev. **12**: 457–514. *f. 1–4*. O 1946.

Jones, H. A. Cytology, genetics and breeding. Problems and progress in onion breeding. Herbertia **11** (1944): 275–294. *pl. 270, 271 + f. 125–127*. 1946.

Little, J. M., Jones, H. A. & Clarke, A. E. Physiology of reproduction. The distribution of the male-sterility gene in varieties of onion. Herbertia **11** (1944): 310–312. *table 1*. 1946.

Lowe, Jeanette & Nelson, Oliver E. Miniature seed—a study in the development of a defective caryopsis in maize. Genetics **31**: 525–533. *f. 1–9*. S 1946.

McLean, Susanne W. Interspecific crosses involving *Datura ceratocaula* obtained

by embryo dissection. Am. Jour. Bot. **33**: 630–638. *tables 1–4 + f. 1–12.* O [N] 1946.

Muller, H. J. A brief comment on mother-daughter chromosomes. [*see* **Prokofieva-Belgovskaja, A. A.**] Jour. Hered. **37**: 246. Au [O] 1946.

Nielsen, Etlar L. Breeding behavior and chromosome numbers in progenies from twin and triplet plants of *Poa pratensis.* Bot. Gaz. **108**: 26–40. *f. 1–34.* 22 O 1946.

Prokofieva-Belgovskaja, A. A. "Mother" and "daughter" chromosomes. Significance of heterocyclic systems in paired nuclei. Jour. Hered. **37**: 239–246. *f. 1–15.* Au [O] 1946.

Smith, Luther. Haploidy in Einkorn. Jour. Agr. Res. **73**: 291–301. *1 f.* 15 O 1946.

Toole, Marguerite G. & Clarke, Alfred E. Chromosome behavior and fertility of colchicine-induced tetraploids in *Allium cepa* and *A. fistulosum.* Herbertia **11** (1944): 295–303. *pl. 272, 273 + f. 128.* 1946.

Warmke, H. E. Sex determination and sex balance in *Melandrium.* Am. Jour. Bot. **33**: 648–660. *f. 1–7 + tables 1–3.* O [N] 1946.

Wilson, G. B. Cytological studies in the Musae. II. Meiosis in some diploid clones. Genetics **31**: 475–482. *26 figs.* S 1946; III. Meiosis in some seedling clones. 483–493. *11 figs.*

PLANT PHYSIOLOGY

Altschul, A. M., Karon, M. L. & Fynn, P. J. An apparatus and method for the measurement of the respiration of cottonseed. Plant Physiol. **21**: 410–415. *f. 1, 2.* O 1946.

Altschul, A. M. *et al.* Effect of inhibitors on the respiration and storage of cottonseed. Plant Physiol. **21**: 573–587. *f. 1–3.* O 1946.

Aronoff, S. Photochemical reduction by chloroplast grana. Plant Physiol. **21**: 393–409. *f. 1–7.* O 1946.

Berry, L. Joe & Brock, Mary Jane. Polar distribution of respiratory rate in the onion root tip. Plant Physiol. **21**: 542–549. O 1946.

Bonner, James. The chemistry and physiology of the pectins. II. Bot. Rev. **12**: 535–537. N 1946.

Brunstetter, Bryon C. *et al.* The chloride content of conifers. Science **104**: 415, 416. 1 N 1946.

Chance, H. L. & Smith, James M. The effects of light, gravity, and centrifugal force upon the tropic responses of buckwheat seedlings. Plant Physiol. **21**: 452–458. O 1946.

Cox, M. J. & MacMasters, M. M. Micromanipulative studies on gelatinized starch granules. Plant Physiol. **21**: 459–466. *f. 1, 2.* O 1946.

De Ropp, R. S. Apparatus for prolonged sterile culture *in vitro* of whole plants or excised plant tissues. Science **104**: 371–373. 18 O 1946.

Dufrenoy, J. & Reed, H. S. The respiratory processes in plant cells in relation to the formation of coacervates. Plant Physiol. **21**: 416–424. *f. 1, 2.* O 1946.

Hammar, Harald E. & Hunter, James H. Some physical and chemical changes in the composition of pecan nuts during kernel filling. Plant Physiol. **21**: 476–491. *f. 1–9.* O 1946.

Hansen, Elmer. Effect of 2,4-dichlorophenoxyacetic acid on the ripening of Bartlett pears. Plant Physiol. **21**: 588–592. *f. 1.* O 1946.

Harrington, James F. The trend of soluble nitrate, phosphate and potassium concentrate in the development of the spinach petiole. Proc. Iowa Acad. **52**: 121–126. *tables 1–3.* 1945 [Jl 1946].